

# A SYNOPSIS OF *MACHAERANTHERA* (ASTERACEAE: ASTEREAEE), WITH RECOGNITION OF SEGREGATE GENERA

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## ABSTRACT

Recent investigations of *Machaeranthera* s.l. incorporating molecular, morphological, cytological, and chemical evidence have supported relationships that do not conform to any recent circumscription of the genus. To bring the classification of *Machaeranthera* more in line with current understanding of its evolutionary history, revisions to its taxonomy are proposed. *Machaeranthera* is circumscribed to include two species, and other species that have been included in *Machaeranthera* are apportioned into three additional genera. *Dieteria* is revived to accommodate three of these species, *Xanthisma* is expanded to accommodate 16 more species, and the new genus *Arida* is proposed for those remaining. New combinations for the species in *Dieteria*, *Xanthisma*, and *Arida* are provided.

## RESUMEN

Investigaciones recientes en *Machaeranthera* s.l. que incluyen datos moleculares, morfológicos, citológicos, y químicos dan como resultado unas relaciones que no concuerdan con ninguna circunscripción reciente del género. Para poner la clasificación de *Machaeranthera* más en línea con el conocimiento actual de su historia evolutiva, se proponen revisiones de su taxonomía. *Machaeranthera* se circunscribe para incluir dos especies, y otras especies que se habían incluido en *Machaeranthera* se redistribuyen en tres géneros adicionales. *Dieteria* se rescata para acomodar tres de estas especies, *Xanthisma* se expande para incluir 16 especies más, y se propone el nuevo género *Arida* para las restantes. Se realizan las nuevas combinaciones para las especies de *Dieteria*, *Xanthisma*, y *Arida*.

The genus *Machaeranthera* Nees (Asteraceae: Astereae) was established to accommodate the single species *M. tanacetifolia* Nees. Since its inception, many different circumscriptions of *Machaeranthera* have been proposed, and the genus has included various parts of several other genera, with little agreement on its composition or its relationships with other taxa (see Morgan and Simpson 1992 for a more detailed taxonomic history).

The most recent published treatment of *Machaeranthera* was by Hartman (1990), who included 36 species in the genus, excluding several taxa that are now placed in the genera *Hazardia* Greene (Hartman 1990), *Rayjacksonia* R.L. Hartman & M.A. Lane (Lane & Hartman 1996), *Tonestus* A. Nelson (Nesom 1991), and *Xylorhiza* Nutt. (Hartman 1990). The circumscription of *Machaeranthera* adopted by Hartman (1990) included species with both cyanic (white, blue, pink, purple) and yellow rays, and apportioned them into two subgenera and eight sections. We will refer to this circumscription as *Machaeranthera* s.l.



Investigations of *Machaeranthera* s.l. using molecular evidence have helped to clarify its systematics. Restriction site data from chloroplast DNA (cpDNA) indicated that *Machaeranthera* section *Psilactis* (A. Gray) Turner & Horne was not a close relative of *Machaeranthera* s.l. (Morgan & Simpson 1992; Morgan 1993). This section was removed from *Machaeranthera* s.l. by Morgan (1993), leaving 30 species in the genus. More recent investigations of *Machaeranthera* (sensu Morgan 1993) employed DNA sequence data from nuclear ribosomal DNA internal and external transcribed spacers (nrDNA) (Morgan 1997; Morgan 2003). Comparison of this evidence with cpDNA data indicated that the evolution of *Machaeranthera* and its relatives has been complex, involving as many as seven occurrences of reticulate evolution. The molecular evidence also indicated that other genera (e.g., *Oönoopsis* Nutt., *Pyrrocoma* Hook., and *Xanthisma* DC.) are closely related to various parts of *Machaeranthera* (Fig. 1).

The relationships supported by a combination of molecular, morphological, cytological, and chemical evidence do not support any recent circumscription of *Machaeranthera*. Therefore, a new classification is needed to bring the taxonomy of the genus more in line with current understanding of its relationships. A case could be made for including *Oönoopsis* and *Pyrrocoma* in an expanded *Machaeranthera*, and cpDNA evidence provides some support for such a treatment (Fig. 1). However, nrDNA data do not support this circumscription (Fig. 1). Furthermore, we contend that enlarging *Machaeranthera* through accretion would obscure the phylogenetic patterns within the complex, and would result in a large, heterogenous, and unwieldy genus that would be difficult to characterize satisfactorily. We therefore propose that *Machaeranthera* (sensu Morgan 1993) be divided into four genera, as described below.

#### KEY TO THE GENERA TREATED HERE

1. Ray floret corollas yellow (heads radiate) \_\_\_\_\_ **Xanthisma**
1. Ray floret corollas white (sometimes yellowish on drying), pink, red-purple, or purple, or heads eradiate.
  2. Leaves deeply pinnatifid to bipinnatifid throughout, at least many of the teeth and lobes sharply acute with bristle tips, bristles 0.2–1 mm long; plants annual; pappus of subulate bristles, dorsio-ventrally flattened near base, bases overlapping \_\_\_\_\_ **Machaeranthera**
  2. Leaves entire to toothed or lobed, if pinnatifid to bipinnatifid throughout then lobes often rounded, with or without an apiculum but not bristle tipped; plants annual to strongly perennial; pappus of filiform to subulate bristles, terete to flattened near base, bases overlapping or not overlapping.
    3. Plants strongly perennial with a branched caudex (taprooted, sometimes biennial in *Xanthisma gymnocephalum*, central Mexico); receptacles covered with scales 0.3–3 mm long, often forming an alveolate reticulum; pappus bristles subulate, flattened near base, bases strongly overlapping \_\_\_\_\_ **Xanthisma**
    3. Plants taprooted annuals or short lived perennials (forming vegetative rosettes in *Arida blepharophylla*, a species also exceptional, as indicated, in the following characters); receptacles usually naked (or scales rarely to 0.5 mm



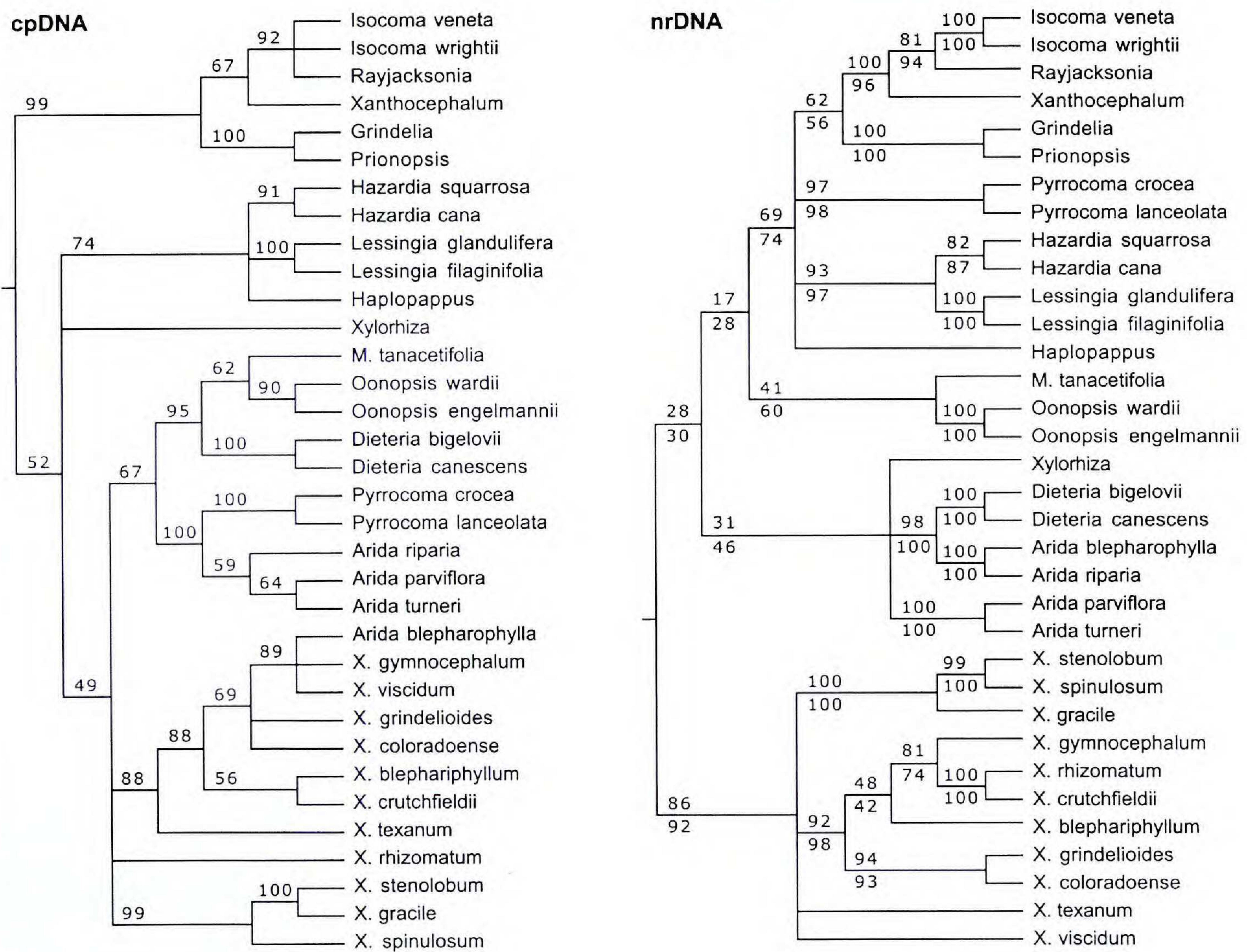


Fig. 1. Strict consensus trees resulting from analysis of chloroplast DNA restriction site data (cpDNA) and combined ITS and ETS sequence data (nrDNA) of *Machaeranthera* and related taxa, from Fig. 3 of Morgan (2003) with modified nomenclature. Bootstrap percentages are shown above and below the branches; values above the branches on both phylogenies are from unweighted bootstrap analysis, and values below the branches on the nrDNA phylogeny are from analyses in which transversions were weighted two times transitions. Generic names for the species of *Machaeranthera* sensu Morgan (1993) conform to the treatment proposed in this paper. Genus names for species of *Machaeranthera* and *Xanthisma* are abbreviated "M." and "X.," respectively.



long); pappus bristles filiform, not flattened near base (or slightly so), bases not (or slightly) overlapping.

4. Ray florets with prominent pappus (often eradiate in the glandular-pubescent *D. canescens* var. *shastensis*); leaves entire to toothed and plants variously pubescent with glandular and/or nonglandular hairs; mountains, plains, and basins of W U.S.A.; SW Canada; extreme N Mexico \_\_\_\_\_ **Dieteria**
4. Ray florets with pappus absent (5 species; eradiate in the glabrous *A. carnosus*) or present; if pappus present then leaves pinnatifid to bipinnatifid throughout or (if leaves entire to toothed) plants glabrous except for bristles or apiculate or bristle tipped teeth on leaf margins; deserts of SW U.S.A.; Mexico \_\_\_\_\_ **Arida**

**Machaeranthera** Nees, Gen. & Sp. Asterearum 224. 1832. TYPE: *Aster tanacetifolius* Kunth.

*Chrysopsis* subgenus *Pappochroma* Nutt., J. Acad. Nat. Sci. Phila. 7:34. 1834. *Dieteria* subgenus *Pappochroma* (Nutt.) Nutt., Trans. Amer. Philos. Soc. 7:302. 1840. *Dieteria* section *Pappochroma* (Nutt.) Walpers, Rep. Bot. Syst. 2:587. 1843. TYPE: *Chrysopsis coronopifolia* Nutt.

*Aster* section *Machaeranthera* (Nees) Benth. & Hook., Gen. Pl. 2:272. 1873. *Aster* subgenus *Machaeranthera* (Nees) A. Gray, Proc. Amer. Acad. Arts 16:99. 1880.

*Machaeranthera* series *Verae* Cronquist & D.D. Keck, Brittonia 9:238. 1957, nom. illeg. (ICBN: 52.1).

**Herbs** taprooted annuals or biennials, 5–100 cm tall. **Stems** erect to ascending, much branched when well developed, moderately to densely pubescent with glandular and nonglandular hairs. **Leaves** alternate; pinnatifid or bipinnatifid, deeply lobed or dissected, moderately to densely pubescent with glandular and nonglandular hairs, apices, including lobes and teeth, mucronate to bristle tipped, bristles if present 0.2–1 mm long. **Heads** radiate. **Involucre**s broadly turbinate to hemispheric. **Phyllaries** in 3–6 imbricate series, graduated in length, appressed, spreading, or reflexed, moderately to densely pubescent with glandular and nonglandular hairs; bases indurate, apices herbaceous. **Receptacles** alveolate, flat to convex, naked or with scales to 0.4 mm long. **Ray florets** pistillate, fertile; corollas blue, violet, or purple. **Disc florets** bisexual, fertile, corollas yellow, narrowly funnelform; tubes and limbs glabrous or glabrate, lobes 0.3–1 mm long, glabrous to pubescent. **Cypselae** of ray and disc florets distinctly dimorphic, narrowly to broadly obovate, sparsely to densely pubescent; moderately thick walled, with 4–9 ribs per face, 2.4–3.8 mm long, those of ray florets ~3 sided, rounded abaxially, of disc florets somewhat compressed laterally; pappus white to tawny, of ray florets 1/2 to nearly equalling length of disc florets; bristles coarsely barbellate, in 1–3 series, dorsi-ventrally flattened and dissimilar in width near base, bases overlapping, mostly 4.5–6.5 mm long.  $n = 4$ .

The circumscription of *Machaeranthera* adopted here results in a genus of two species. We apportion the remaining 28 species of *Machaeranthera* (sensu Morgan 1993) to *Dieteria*, *Xanthisma*, and *Arida* (see below). The three species placed in *Dieteria* could potentially also be included in *Machaeranthera* because of a number of similarities. All members of the two genera produce flavonols, and all have chromosome numbers of  $n = 4$ , obovate fruits, and nar-



row phyllaries that are often reflexed (Hartman 1976, 1990; Turner 1987). This relationship was also supported by cpDNA evidence (Fig. 1). However, nrDNA evidence conflicted with cpDNA (Fig. 1), and the substantial conflict between them complicates the issue by suggesting reticulate evolution in the ancestors of *Machaeranthera*, *Dieteria*, or both. In addition, cpDNA and nrDNA evidence both supported a close relationship between *Machaeranthera* and *Oönoopsis*, and expansion of *Machaeranthera* to include *Dieteria* would also have to include *Oönoopsis*, which differs from *Machaeranthera* in many ways (Morgan & Simpson 1992). Additional synonymy for *Machaeranthera* is included in Turner (1987).

#### KEY TO THE SPECIES OF MACHAERANTHERA

1. Involucres hemispheric; herbaceous phyllary apices spreading to reflexed; disc corolla lobes mostly 0.3–0.7 mm long, glabrous or glabrate \_\_\_\_\_ **1. *Machaeranthera tanacetifolia***
1. Involucres broadly turbinate; herbaceous phyllary apices appressed; disc corolla lobes mostly 0.7–1 mm long, pubescent \_\_\_\_\_ **2. *Machaeranthera tagetina***

**1. *Machaeranthera tanacetifolia*** (Kunth) Nees, Gen. & Sp. Asterearum 225. 1832. *Aster tanacetifolius* Kunth, Nov. Gen. & Sp., ed. folio, 4:74. 1820. *Aster chrysanthemoides* Willd. ex Spreng., Syst. Veg. 3:538. 1826. TYPE: MEXICO: "Colitur in horto Mexicano," s.d., *Humboldt s.n.* (HOLOTYPE: P nv, IDC microfiche 6209. 97.III.6; possible ISOTYPE: B-W; PHOTOISOTYPE: TEX!).

*Chrysopsis coronopifolia* Nutt., J. Acad. Nat. Sci. Phila. 7:34. 1834. *Dieteria coronopifolia* (Nutt.) Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:302. 1840. *Machaeranthera coronopifolia* (Nutt.) A. Nelson, Bot. Gaz. 37:268. 1904. TYPE: U.S.A. NORTH DAKOTA: "Towards the sources of the Missouri" (probably near Fort Mandon), Jul–Aug 1811, *Nuttall s.n.* (ISOTYPE: GH; probable ISOTYPE: NY).

**2. *Machaeranthera tagetina*** Greene, Pittonia 4:71. 1899. *Aster tagetinus* (Greene) S.F. Blake, Contr. U.S. Natl. Herb. 25:263. 1925. TYPE: U.S.A. ARIZONA. Cochise Co.: near Fort Huachuca, 1891, *Wilcox s.n.* (HOLOTYPE: US).

***Dieteria*** Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:300. 1840. LECTOTYPE, here designated: *Aster canescens* Pursh.

*Machaeranthera* section *Hesperastrum* A. Gray, Proc. Amer. Acad. Arts 6:539. 1865. *Aster* subgenus *Hesperastrum* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 16:97. 1880. *Aster* section *Hesperastrum* (A. Gray) A. Gray, Syn. Fl. N. Amer. 1(2):174. 1884. TYPE: *Machaeranthera shastensis* A. Gray.

*Machaeranthera* subgenus *Dieteria* (Nutt.) Greene, Pittonia 3:59. 1896.

*Machaeranthera* series *Variabiles* Cronquist & D.D. Keck, Brittonia 9:237. 1957, nom. illeg. (ICBN: 24.3).

**Herbs** taprooted annuals, biennials, or perennials, 10–100 cm tall. **Stems** erect to ascending, much branched when well developed, glabrous to variously pubescent with glandular and/or nonglandular hairs. **Leaves** alternate; entire to irregularly serrate or dentate, moderately to densely pubescent with glandular



and/or nonglandular hairs, apices, including lobes and teeth, spinescent due to indurated apiculae, bristles absent. **Heads** radiate or eradiate. **Involucre** turbinate, campanulate, or hemispheric. **Phyllaries** in 3–12 imbricate to subimbricate series, graduated in length, appressed, spreading, or reflexed, glabrous or variously pubescent with glandular and/or nonglandular hairs; bases indurate, apices herbaceous, margins scarious. **Receptacles** alveolate, convex, naked or scales to 0.3 mm long. **Ray florets** pistillate, fertile (sterile or absent in *D. canescens* var. *shastensis*); corollas white, blue, violet, or purple. **Disc florets** bisexual, fertile, corollas yellow,  $\pm$  funnellform, tubes and limbs glabrous or glabrate, lobes 0.2–0.7 mm long, glabrous to minutely pubescent. **Cypselae** of ray and disc florets somewhat dimorphic, linear to obovate, glabrous to moderately pubescent; thin walled, smooth or with 4–6 ribs per face, 3–6 mm long, those of ray florets generally flattened, rounded abaxially, of disc florets flattened laterally; pappus white to brown or reddish brown, of ray florets 2/3 to nearly equalling length of disc florets; bristles somewhat barbellate, in 1–3 series, at most somewhat dorsi-ventrally flattened and dissimilar in width near base, bases not to slightly overlapping, mostly 4–8 mm long.  $n = 4$ .

Although similar to *Machaeranthera* in several ways (see above), the members of *Dieteria* may be distinguished from it by foliage and fruit characters. *Dieteria* has entire to serrate or dentate leaves with thin-walled fruits that are mostly longer than 3 mm, while *Machaeranthera* has leaves that are deeply lobed or dissected and thick-walled fruits that are mostly 3 mm or less long. There is a great deal of morphological variation in *Dieteria*, which has resulted in a large number of species names. The treatment adopted here follows that of Turner (1987) in recognizing three species containing 16 varieties, with 3 varieties in *D. asteroides*, 3 in *D. bigelovii*, and 10 in *D. canescens*. Additional synonymy for *Dieteria* is included in Turner (1987).

#### KEY TO THE SPECIES OF DIETERIA

1. Phyllaries and peduncles both with prominent glandular pubescence.
  2. Leaves covered with stiff glandular hairs \_\_\_\_\_ **1. *Dieteria asteroides*** (var. ***glandulosa***)
  2. Leaves glabrous to variously pubescent, but not covered with stiff glandular hairs.
    3. Midstem leaves linear-lanceolate to linear or linear-oblongate (ovate to obovate in var. *leucanthemifolia*), 1.5–5 mm wide; herbaceous phyllary apices acute to acuminate (1–3 mm long) \_\_\_\_\_ **3. *Dieteria canescens***
    3. Differing from the above in at least one respect; midstem leaves lanceolate to oblongate and 5–15 mm wide, or herbaceous phyllary apices long-acuminate (2–6 mm long), or both \_\_\_\_\_ **2. *Dieteria bigelovii***
1. Phyllaries and peduncles variously pubescent with glandular and/or nonglandular hairs, but rarely with prominent glandular pubescence on both.
  4. Phyllaries usually pubescent throughout, with pubescence on both herbaceous apices and indurate bases, apices acute to long-acuminate, 1–6 mm long; midstem leaves 6–20 mm wide (2–6 mm in var. *lagunensis*) \_\_\_\_\_ **1. *Dieteria asteroides***
  4. Phyllaries only occasionally pubescent throughout, with pubescence mostly con-



fined to herbaceous apices, apices acute to acuminate, 1–3 mm long; mid-stem leaves 1.5–6(–8) mm wide \_\_\_\_\_

**3. *Dieteria canescens***

**1. *Dieteria asteroides*** Torr., in Emory Report 142. 1848. *Machaeranthera asteroides* (Torr.) Greene, Pittonia 3:63. 1896. TYPE: U.S.A. NEW MEXICO: “elevated land between the Del Norte and the waters of the Gila,” 16 Oct 1847, Emory s.n. (HOLOTYPE: NY).

*Machaeranthera canescens* var. *latifolia* A. Gray, Pl. Wright. 2:75. 1853. *Aster canescens* var. *latifolia* (A. Gray) A. Gray, Syn. Fl. N. Amer. 1(2):206. 1884. TYPE: U.S.A. New Mexico: “Near the copper mines,” Sep–Oct 1851, C. Wright 1152 (LECTOTYPE: GH [designated by Turner 1987]; ISOLECTOTYPES: GH, MO, NY, PH, UC, US).

*Aster canescens* Pursh var. *tephrodes* A. Gray, Proc. Amer. Acad. Arts 16:99. 1880. *Machaeranthera tephrodes* (A. Gray) Greene, Pittonia 4:24. 1899. *Aster tephrodes* (A. Gray) S.F. Blake, Contr. U.S. Natl. Herb. 25:563. 1925. Typification unclear: In Bot. Calif. 1:322. 1876, Gray mistakenly based the name *Aster incanus* (Lindl.) A. Gray on *Diplopappus incanus* Lindl. for plants occurring in southern California. He subsequently corrected this mistake and proposed the name *Aster canescens* var. *tephrodes* for these plants, noting that they also occurred in Arizona and New Mexico. Although stating that *A. c.* var. *tephrodes* “...was named *A. incanus* in the Botany of California, but...cannot be Lindley’s plant,” Gray apparently did not select a type specimen for *Aster canescens* var. *tephrodes*. The only material mentioned by Gray in connection with any of these names was collected by “Capt. E.K. Smith” in “Guadalupe Canyon, Sonora,” but we have not been able to locate the specimens. Turner (1987) placed *Aster incanus*, *Aster canescens* var. *tephrodes*, *Machaeranthera tephrodes*, and *Aster tephrodes* in synonymy under *Machaeranthera canescens* var. *incana*.

KEY TO THE VARIETIES OF *DIETERIA ASTEROIDES*

1. Stems glabrous to glandular-pubescent; leaves covered with stiff glandular hairs \_\_\_\_\_ **1b. *D. asteroides* var. *glandulosa***
1. Stems pubescent, puberulent, or canescent, glandular pubescence sparse or lacking; leaves puberulent or canescent, stiff glandular hairs sparse or lacking.
  2. Involucres hemispheric; herbaceous phyllary apices long-acuminate, 3–6 mm long; mid-stem leaves 6–20 mm wide, usually clearly serrate or serrulate \_\_\_\_\_ **1a. *D. asteroides* var. *asteroides***
  2. Involucres broadly turbinate (rarely hemispheric); herbaceous phyllary apices acute to acuminate, 1–3 mm long; mid-stem leaves 2–6 mm wide, entire to slightly serrulate \_\_\_\_\_ **1c. *D. asteroides* var. *lagunensis***

**1a. *Dieteria asteroides* var. *asteroides***

**1b. *Dieteria asteroides* var. *glandulosa*** (B.L. Turner) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera asteroides* (Torr.) Greene var. *glandulosa* B.L. Turner, Phytologia 60:77. 1986. TYPE: U.S.A. ARIZONA. Maricopa Co.: U.S. highway 60, 2.6 mi E of Queen Creek tunnel, 4200 ft, 19 Sep 1975, Pinkava, Keil & Lehto L18904 (HOLOTYPE: LL!; ISOTYPES: ASU, CSU, NY).

**1c. *Dieteria asteroides* var. *lagunensis*** (D.D. Keck) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera lagunensis* D.D. Keck, Brittonia 9:238. 1957. *Machaeranthera asteroides* (Torr.) Greene var. *lagunensis* (D.D. Keck) B.L. Turner, Phytologia 60:77. 1986. TYPE: U.S.A. CALIFORNIA. San Diego Co.: 2 mi S of the main recreation area, Laguna Mountains, 5200 ft, 20 Aug 1952, P.A. Munz & E.K. Balls 17948 (HOLOTYPE: NY; ISOTYPE: RSA).



- 2. *Dieteria bigelovii*** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Aster bigelovii* A. Gray, Pacific Railway Survey 4:97. 1857. *Machaeranthera bigelovii* (A. Gray) Greene, Pittonia 3:63. 1896. TYPE: U.S.A. NEW MEXICO. Bernalillo Co.: "arroyos in the Sandia Mountains," 10 Oct 1853, J.M. Bigelow s.n. (HOLOTYPE: GH; ISOTYPE: NY).

KEY TO THE VARIETIES OF *DIETERIA BIGELOVII*

1. Involucres hemispheric, 2–3 times broad as tall; phyllaries 90–100, mostly 0.5–1 mm wide at midpoint, herbaceous apices long-acuminate, 2–5 mm long \_\_\_\_\_ **2c. *D. bigelovii* var. mucronata**
1. Involucres broadly turbinate to hemispheric, 1–2(–3) times broad as tall, phyllaries 25–100, mostly 1–2 mm wide at midpoint, herbaceous apices acute to long-acuminate, 2–6 mm long.
2. Phyllaries 25–50, apices acute to acuminate, 2–4 mm long; ray florets 12–30 \_\_\_\_\_ **2b. *D. bigelovii* var. commixta**
2. Phyllaries 50–100, apices long-acuminate, 3–6 mm long; ray florets 30–60 \_\_\_\_\_ **2a. *D. bigelovii* var. bigelovii**

**2a. *Dieteria bigelovii* var. bigelovii**

- 2b. *Dieteria bigelovii* var. commixta** (Greene) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera commixta* Greene, Pittonia 4:71. 1899. *Machaeranthera canescens* (Pursh) A. Gray var. *commixta* (Greene) S.L. Welsh, Great Basin Naturalist 43:316. 1983. *Machaeranthera bigelovii* (A. Gray) Greene var. *commixta* (Greene) B.L. Turner, Phytologia 60:77. 1986. TYPE: U.S.A. UTAH. Garfield Co.: Henry Mountains, Bromide Pass, 10,000 ft, 27 Jul 1894, M.E. Jones 5695y (HOLOTYPE: US; ISOTYPE: POM).

- 2c. *Dieteria bigelovii* var. mucronata** (Greene) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera mucronata* Greene, Pittonia 4:72. 1899. *Aster adenolepis* S.F. Blake, J. Wash. Acad. Sci. 30:471. 1940, nom. nov., non *Aster mucronatus* Sheldon, 1903. *Machaeranthera bigelovii* (A. Gray) Greene var. *mucronata* (Greene) B.L. Turner, Phytologia 62:238. 1987. TYPE: U.S.A. ARIZONA. Coconino Co.: Thompson Canyon, 8500 ft, 19 Sep 1894, M.E. Jones 6065bl (LECTOTYPE: US [designated by Turner 1987]).

- 3. *Dieteria canescens*** (Pursh) Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:300. 1840. BASIONYM: *Aster canescens* Pursh, Fl. Amer. Sept. 2:547, 1813. *Machaeranthera canescens* (Pursh) A. Gray, Pl. Wright. 1:89. 1852. TYPE: U.S.A. NORTH DAKOTA: "on the denuded banks of the Missouri" (vicinity of Fort Mandon), 1811, Nuttall s.n. (HOLOTYPE: BM; possible ISOTYPE: NDG).

*Dieteria viscosa* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:301. 1840. *Aster canescens* Pursh var. *viscosus* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 16:99. 1880. *Machaeranthera viscosa* (Nutt.) Greene, Pittonia 4:22. 1899. *Machaeranthera canescens* (Pursh) A. Gray var. *viscosa* (Nutt.) Piper, Contr. U.S. Natl. Herb. 11:576. 1905. TYPE: U.S.A. NEBRASKA. Scotts Bluff Co.: "near Scott's Bluff, on the Platte," 1834, Nuttall s.n. (HOLOTYPE: BM).

*Dieteria divaricata* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:301. 1840. *Machaeranthera divaricata* (Nutt.) Greene, Pittonia 4:23. 1899. TYPE: U.S.A.: "denudated plains of the Rocky Mountains and Oregon, common," 1834, Nuttall s.n. (HOLOTYPE: GH).

*Dieteria pulverulenta* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:300. 1840. *Machaeranthera*



*pulverulenta* (Nutt.) Greene, Pittonia 4:23. 1899. TYPE: U.S.A.: "arid plains towards the sources of the Platte," 1834, *Nuttall s.n.* (HOLOTYPE: PH).

*Machaeranthera laetevirens* Greene, Pittonia 3:61. 1896. *Aster leiodes* Blake, Contr. U.S. Natl. Herb. 25:563. 1925, nom. nov., non *Aster laetevirens* Greene (1900). TYPE: U.S.A. NEVADA. Elko Co.: Clover Mountains, 26 Jul 1894, *E.L. Greene s.n.* (HOLOTYPE: NDG; ISOTYPE: NDG).

*Machaeranthera latifolia* A. Nelson, Proc. Biol. Soc. Wash. 20:38. 1907. *Machaeranthera canescens* (Pursh) A. Gray var. *latifolia* (A. Nelson) S.L. Welsh, Great Basin Naturalist Mem. 9:213. 1987. *Machaeranthera canescens* (Pursh) A. Gray var. *monticola* Dorn, Vascular Pl. Wyo. 295. 1988. TYPE: U.S.A. UTAH. Salt Lake Co.: Big Cottonwood Canyon, 8950 ft, 9 Aug 1933, *A. O. Garrett 1933* (HOLOTYPE: RM!; ISOTYPES: GH, LLI, US).

#### KEY TO THE VARIETIES OF *DIETERIA CANESCENS*

1. Phyllaries spreading to reflexed, rarely appressed.
  2. Involucres mostly (9–)10–16 mm tall.
    3. Suffruticose perennials; involucres (10–)12–16 mm tall; phyllary apices densely glandular \_\_\_\_\_ **3f. *D. canescens*** var. **ziegleri**
    3. Biennials or short-lived perennials; involucres (9–)10–15 mm tall; phyllary apices densely appressed-pubescent, glands if present obscured by appressed pubescence \_\_\_\_\_ **3j. *D. canescens*** var. **nebraskana**
  2. Involucres mostly 6–10(–12) mm tall.
    4. Stems canescent; glandular pubescence sparse or lacking.
      5. Plants usually with a single stiffly erect stem; branches stiff and straight, widely divaricate \_\_\_\_\_ **3b. *D. canescens*** var. **incana**
      5. Plants with a single stem or with multiple ascending stems; branches flexible and curved, loosely spreading or (usually) ascending but not widely divaricate.
        6. Ray florets sterile or absent; phyllaries 3–5(–7) seriate \_\_\_\_\_ **3e. *D. canescens*** var. **shastensis**
        6. Ray florets pistillate and fertile; phyllaries 5–10 seriate \_\_\_\_\_ **3a. *D. canescens*** var. **canescens**
    4. Stems evidently glandular, frequently also puberulent or canescent, occasionally glabrous.
      7. Stems canescent, glands usually sessile or subsessile; most heads sessile or with peduncles shorter than involucre height \_\_\_\_\_ **3d. *D. canescens*** var. **sessiliflora**
      7. Stems with prominent stipitate glands, also occasionally puberulent or canescent; most peduncles longer than involucre height.
        8. Midstem and upper leaves ovate, oblong or obovate, 1.5–4 times longer than wide \_\_\_\_\_ **3c. *D. canescens*** var. **leucanthemifolia**
        8. Midstem and upper leaves linear-lanceolate to linear, more than 4 times longer than wide \_\_\_\_\_ **3h. *D. canescens*** var. **aristata**
1. Phyllaries appressed or occasionally spreading, rarely reflexed.
  9. Ray florets sterile or absent \_\_\_\_\_ **3e. *D. canescens*** var. **shastensis**
  9. Ray florets pistillate and fertile.
    10. Phyllaries densely appressed-pubescent, glandular pubescence lacking or sparse and obscured by appressed pubescence \_\_\_\_\_ **3g. *D. canescens*** var. **ambigua**
    10. Phyllaries glabrous to glandular-pubescent, rarely appressed-pubescent or canescent.
      11. Stems with prominent stipitate glands, occasionally also canescent, rarely glabrous \_\_\_\_\_ **3h. *D. canescens*** var. **aristata**



11. Stems glabrous to puberulent or canescent, stipitate glands sparse or lacking \_\_\_\_\_ **3i D. canescens** var. **glabra**

**(i) Dieteria canescens** subsp. **canescens**

**3a. Dieteria canescens** var. **canescens**

**3b. Dieteria canescens** var. **incana** (Lindl.) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Diplopappus incanus* Lindl., Bot. Reg. 20:t. 1693, 1834. *Dieteria incana* (Lindl.) Torr. & A. Gray, Fl. N. Amer. 2:100. 1841. *Machaeranthera canescens* (Pursh) A. Gray var. *incana* (Lindl.) A. Gray, Bot. Wilkes Exp. Phan. 17(2):340. 1874. *Machaeranthera incana* (Lindl.) Greene, Pittonia 3:62. 1896. TYPE: U.S.A. OREGON: "Columbia River," described from seeds grown in London, 1830, Douglas s.n. (HOLOTYPE: BM; ISOTYPE: GH; ISOTYPE, microfiche: G-DC).

**3c. Dieteria canescens** var. **leucanthemifolia** (Greene) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Aster leucanthemifolius* Greene, Erythea 3:119. 1895. *Machaeranthera leucanthemifolia* (Greene) Greene, Pittonia 3:61. 1896. *Machaeranthera canescens* (Pursh) A. Gray var. *leucanthemifolia* (Greene) S.L. Welsh, Great Basin Naturalist 43:316. 1983. TYPE: U.S.A. NEVADA. Esmeralda Co.: near Candelaria, 6000 ft, Jun 1886, W.H. Shockley 268 (HOLOTYPE: CAS; ISOTYPES: DS, US).

**3d. Dieteria canescens** var. **sessiliflora** (Nutt.) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Dieteria sessiliflora* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:301. 1840. *Machaeranthera sessiliflora* (Nutt.) Greene, Pittonia 3:60. 1896. *Machaeranthera canescens* (Pursh) A. Gray var. *sessiliflora* (Nutt.) B.L. Turner, Phytologia 60:78. 1986. TYPE: U.S.A. IDAHO(?): "Denudated plains of the Rocky Mountains and Oregon," 1836, Nuttall s.n. (HOLOTYPE: BM).

**3e. Dieteria canescens** var. **shastensis** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera shastensis* A. Gray, Proc. Amer. Acad. Arts 6:539. 1866. *Aster shastensis* (A. Gray) A. Gray, Bot. Calif. 1:322. 1876. *Machaeranthera canescens* (Pursh) A. Gray var. *shastensis* (A. Gray) B.L. Turner, Phytologia 60:79. 1986. TYPE: U.S.A. CALIFORNIA. Siskiyou Co.: Mt. Shasta, 9000 ft, 1860-62, W.H. Brewer 1385 (HOLOTYPE: GH; ISOTYPE: US).

**3f. Dieteria canescens** var. **ziegleri** (Munz) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera canescens* (Pursh) A. Gray subsp. *ziegleri* Munz, Aliso 7:65. 1969. *Machaeranthera canescens* (Pursh) A. Gray var. *ziegleri* (Munz) B.L. Turner, Phytologia 60:79. 1986. TYPE: U.S.A. CALIFORNIA. Riverside Co.: N side of Santa Rosa Mountain, 6500-7500 ft, 30 Sep 1968, L.B. Ziegler s.n. (HOLOTYPE: RSA; ISOTYPE: CAS).

**(ii) Dieteria canescens** subsp. **glabra** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. *Machaeranthera canescens* (Pursh) A. Gray var. *glabra* A. Gray, Pl. Wright. 1:89. 1852. *Machaeranthera canescens* (Pursh) A. Gray subsp. *glabra* (A. Gray) B.L. Turner, Phytologia 62:239. 1987.

**3g. Dieteria canescens** var. **ambigua** (B.L. Turner) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera canescens* (Pursh) A. Gray var. *ambigua* B.L. Turner, Phytologia 60:77. 1986. TYPE: U.S.A. ARIZONA. Coconino Co.: Flagstaff,



28 Aug 1922, *H. Hanson* A7 (HOLOTYPE: TEX!; ISOTYPES: ARIZ, F, MO, NEB, NY, OSU, PHIL, RM!, TEX!).

- 3h. *Dieteria canescens* var. *aristata*** (Eastwood) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Aster canescens* Pursh var. *aristatus* Eastwood, Proc. Calif. Acad. Sci., ser. 2, 6:296. 1896. *Machaeranthera canescens* (Pursh) A. Gray var. *aristata* (Eastwood) B.L. Turner, Phytologia 60:78. 1986. TYPE: U.S.A. UTAH. San Juan Co.: Willow Creek, 14 Jul 1895, A. Eastwood 45 (HOLOTYPE: CAS).

*Machaeranthera rigida* Greene, Pittonia 4:25. 1899. TYPE: U.S.A. ARIZONA. Navajo Co.: "Kearn's Canyon," 20 Aug 1897, Zuck 41 (HOLOTYPE: NDG).

- 3i. *Dieteria canescens* var. *glabra*** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera canescens* (Pursh) A. Gray var. *glabra* A. Gray, Pl. Wright. 1:89. 1852. *Aster canescens* Pursh var. *viridis* A. Gray, Proc. Amer. Acad. Arts 16:99. 1880. TYPE: U.S.A. NEW MEXICO. Dona Ana Co.: Rio Grande Valley at Presidio San Elizario on sand-bars, 22 Sep 1849, C. Wright 262 (field no. 1258) (LECTOTYPE: GH [designated by Turner 1987]; ISOLECTOTYPES: GH, MO, UC).

*Machaeranthera linearis* Greene, Bull. Torrey Bot. Club 24:511. 1897, non *Machaeranthera linearis* Rydb. 1900. *Aster linearis* (Greene) Cory, Rhodora 38:407. 1936. TYPE: U.S.A. NEW MEXICO. Dona Ana Co.: Mesilla Valley, 3900 ft, 6 Sep 1897, E.O. Wooton 444 (LECTOTYPE: NDG [designated by Turner 1987]; ISOLECTOTYPES: DS, GH, MO, NY, RM!, UC, US).

- 3j. *Dieteria canescens* var. *nebraskana*** (B.L. Turner) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera canescens* (Pursh) A. Gray var. *nebraskana* B.L. Turner, Phytologia 60:78. 1986. TYPE: U.S.A. NEBRASKA. Sheridan Co.: 2 mi E Ellsworth, sandhill prairie on dry, loose sand, 27 Aug 1968, S. Stephens 28307 (HOLOTYPE: NY; ISOTYPES: ARIZ, DS, GH).

***Xanthisma*** DC., Prodr. 5:94. 1836. TYPE: *Xanthisma texanum* DC.

*Eriocarpum* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:320. 1840. TYPE: *Eriocarpum grindelioides* Nutt.

*Sideranthus* Nutt. ex C. Nees in M. Wied-Neuwied, Reise Nord-America 2:440. 1841. TYPE: *Amellus spinulosus* Pursh.

*Centaureidum* Torr. & A. Gray, Fl. N. Amer. 2:246. 1842. TYPE: *Centaureidum drummondii* Torr. & A. Gray.

*Dieteria* subgenus *Sideranthus* (Nutt. ex Nees) Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:301. 1840.

*Machaeranthera* subgenus *Sideranthus* (Nutt. ex Nees) R.L. Hartman, Phytologia 68:456. 1990.

There has been disagreement on the dates of publication for *Eriocarpum* and *Sideranthus*. For example, Farr, Leussink, and Stafleu (1979) give them as Oct-Dec 1840 and 1840, respectively. According to Greene (1895), Nuttall's treatment (p.320) of *Eriocarpum* appeared in 1840 (for pp. 283-356). Subsequently, *Sideranthus* was published by C. Nees in 1841 (Stafleu & Cowan 1981, p. 707).

**Herbs** taprooted annuals, biennials, or perennials, if perennial usually with a much-branched, woody caudex or rhizomatous (forming loose colonies in *X. rhizomatum*), 3-100 cm tall. **Stems** erect or spreading or sprawling, often much branched, glabrous or moderately to densely pubescent with glandular or nonglandular hairs. **Leaves** alternate; entire to serrate, dentate, pinnatifid, or



bipinnatifid, moderately to densely pubescent with glandular or nonglandular hairs, apices, including lobes and teeth, apiculate to bristle tipped, bristles if present 1–4 mm long. **Heads** radiate or eradiate. **Involucres** turbinate, campanulate, or hemispheric. **Phyllaries** in 2–8 imbricate series, graduated in length, appressed, spreading, or reflexed, glabrous or moderately to densely pubescent with glandular or nonglandular hairs; bases indurate, apices herbaceous or achlorophyllous, stiff, leathery, or margins scarious. **Receptacles** alveolate, flat to convex, scales laciniate, 0.3–3 mm long, often forming a reticulum. **Ray florets** pistillate, fertile (absent in *X. grindelioides*, *X. johnstonii*, *X. restiforme*); corollas white, pink, red-purple, purple, or yellow. **Disc florets** bisexual, fertile, corollas yellow, ± funnellform, tubes and limbs glabrous to somewhat pubescent, lobes 0.4–0.9 mm long, glabrous to pubescent. **Cypselae** of ray and disc florets distinctly dimorphic, elliptic to obovate, oblong, or obscurely cordate, sparsely to densely pubescent; thin to thick walled, with 3–9 nerves or ribs per face, (1–)1.5–3.5 mm long, those of ray florets, if present, ± 3 sided, rounded abaxially, of disc florets compressed laterally; pappus usually whitish to brown or reddish brown, of ray florets 1/2 to nearly equaling length of disc florets; bristles coarsely barbellate, in 2–4 series, dorsi-ventrally flattened and dissimilar in width near base, bases overlapping, mostly 3.5–8 mm long.  $n = 2, 3, 4, 8$ .

As defined here, the genus *Xanthisma* consists of the former *Machaeranthera* sections *Blepharodon*, *Sideranthus*, *Havardii*, and *Stenoloba*, plus the unispecific genus *Xanthisma*, which because of the rule of priority becomes the name of the genus. The grouping of *Xanthisma* and these four sections of *Machaeranthera* (sensu Morgan 1993) was well supported by nrDNA evidence (Morgan 2003), and, except for *Arida blepharophylla* (see discussion below), cpDNA evidence did not support any conflicting relationships (Fig. 1). Although *Xanthisma* includes species with both cyanic (blue, purple, pink, or white) and yellow rays, several other morphological characteristics are shared by its members, including short, turbinate, thick-walled fruits that are densely pubescent, receptacular scales, leaves with marginal spines, and chromosome numbers based on  $x = 4$ . Many of these species have in fact been grouped together at the generic or sectional level by authors such as Greene (1894) and Hall (1928).

The following key is based largely on data from Hartman (1976, 1990) and Semple (1974).

#### KEY TO THE SPECIES OF *XANTHISMA*

1. Inner phyllaries, at least, with a basal "stalk," abruptly enlarged into an ovate to orbicular or elliptic blade, mostly 2–5 mm wide and glabrous; apices abruptly acuminate to obtuse, or broadly rounded, not bristle-tipped \_\_\_\_\_ **1. *Xanthisma texanum***
1. Inner phyllaries, as with all, not markedly expanded above, linear to broadly oblong or lanceolate, mostly 1–2 mm wide; apices narrowly obtuse to long-attenuate, usually bristle-tipped.



2. Ray florets absent.
  3. Primary cauline leaves mostly 1–6 cm long, if shorter or absent then plants with several single headed stems arising from a cushion of basal leaves; stems lacking axillary rosettes; NW New Mexico and N Arizona to S Canada \_\_\_\_\_ **5. *Xanthisma grindelioides***
  3. Primary cauline leaves 0.2–1 cm long, basal leaves not persisting on mature plants; stems covered by axillary rosettes of tiny leaves; Coahuila and Nuevo León, Mexico.
    4. Main stem leaves on new growth oblong to narrowly lanceolate; stems canescent to slightly tomentose, the pubescence increasing the stem diameter but slightly; plants much branched and bushy with flexible stems \_\_\_\_\_ **8. *Xanthisma johnstonii***
    4. Main stem leaves deltoid to narrowly triangular; stems densely woolly-tomentose, the pubescence increasing the stem diameter 2 to 3 times; plants divergently but sparingly branched with rigid, rope-like stems \_\_\_\_\_ **9. *Xanthisma restiforme***
2. Ray florets present.
  5. Ray floret corollas white, pink, purple, or lavender.
    6. Plants dwarf, arising from a cluster of basal leaves; stems leafy, up to 12 cm tall, few to several, each 1 headed; montane to alpine, Colorado and S Wyoming \_\_\_\_\_ **3. *Xanthisma coloradoense***
    6. Plants usually robust, basal leaves usually not persisting on the mature plant; stems not always leafy, mostly 15 to 40 cm tall, often branched, each with 1 to 10 or more heads; central NM, W Texas; N half of Mexico.
      7. Plants biennial or short-lived perennial herbs from a normal taproot; ray flowers pink, purple, or lavender (often fading on old specimens); peduncles moderately to densely glandular-stipitate, often with long flexuous hairs intermixed; phyllaries usually herbaceous in upper half, long-attenuate, reflexed or widely spreading; highlands, central Mexico to S edge of the Chihuahuan Desert \_\_\_\_\_ **6. *Xanthisma gymnocephalum***
      7. Plants perennial from a woody, branched caudex, often with a thickened taproot; ray flowers white (rarely purple in *X. gypsophilum*), often with pink or purple streaks on the underside; peduncles villous, hispid, or glandular-stipitate; phyllaries not herbaceous above but with a green or purple strip or patch in the upper half, the tips acute to broadly acuminate, appressed to squarrose; Chihuahuan Desert and vicinity and mountains of W Texas and S New Mexico.
        8. Peduncles and leaves moderately to densely villous; leaves crowded on the lower half to two-thirds of the stem, not greatly reduced in size above (except for 1 or 2 reduced bracts); flowering stems usually unbranched, bearing only one head \_\_\_\_\_ **4. *Xanthisma crutchfieldii***
        8. Peduncles and leaves glandular-stipitate and/or hispid to hispidulose; leaves evenly distributed along the stem usually for well over two-thirds its length, often markedly though gradually reduced in size above; flowering stems often at least sparingly branched with 1 to 10 or more heads.
          9. Peduncles stipitate-glandular; leaves serrate, often coarsely so with 5 to 14 pairs of teeth; SE New Mexico, W Texas; N Mexico \_\_\_\_\_ **7. *Xanthisma gypsophilum***
          9. Peduncles hispid or hispidulose; leaves usually finely or obscurely



- serrate or serrulate, usually with 12 to 25 pairs of teeth; south-central New Mexico to W Texas \_\_\_\_\_ **2. Xanthisma blephariphyllum**
5. Ray floret corollas yellow.
10. Plants growing in loose colonies with stems arising from 3 to 10 or more elongate (2–15 cm or more long), branched rhizomes, 1.5–6 mm in diameter, arising from a woody rootstock; leaves without glands \_\_\_\_\_ **10. Xanthisma rhizomatum**
10. Plants from a taproot or woody caudex, not rhizomatous; leaves often glandular.
11. Cypselae of disc florets broadly obovate to obscurely and narrowly cordate, the thick, bony walls with 10–12 prominent ribs, densely pubescent, margins thickened; pappus mostly of subulate, markedly dorsoventrally flattened bristles 2–3 mm long; plants annual; leaves deeply pinnatifid or bipinnatifid; SW Chihuahua, Mexico \_\_\_\_\_ **15. Xanthisma stenolobum**
11. Cypselae of disc florets oblong to narrowly obovate, walls usually thin, flexible, smooth or with 6–16 obscure ribs, glabrous to moderately pubescent, margins not thickened; pappus of filiform, only slightly flattened bristles 3.5–7 mm long; plants annual to perennial; leaves entire to bipinnatifid; occurring elsewhere.
12. Plants taprooted, annual; phyllaries obtuse to broadly acute, not bristle tipped; leaves serrate or dentate, the teeth blunt or terminating in a stiff callosity, not bristle tipped; cypselae oblong or narrowly elliptic with 12–14 barely discernible nerves, sparsely pubescent; lowlands of SE New Mexico and W Texas \_\_\_\_\_ **17. Xanthisma viscidum**
12. Plants perennial with much-branched caudices, if taprooted annuals then phyllaries with narrowly acute to acuminate and prominently bristle tipped apices; leaves various, if serrate or dentate, the teeth bristle tipped; cypselae elliptic to narrowly obovate with 6–16 weak ribs, glabrous to moderately pubescent; Canada to S U.S.; Mexico.
13. Plants annual with herbaceous stems and bases; involucre glandular.
14. Leaves with entire margins, not bristle lined, or lower cauline and basal ones tridentate or sometimes pinnatifid; phyllaries tipped by bristles 0.1–0.3 mm long; NE Baja California, Mexico \_\_\_\_\_ **16. Xanthisma wigginsii**
14. Leaves uniformly spinulose toothed or lobed, bristles usually 1.5–3 mm long; phyllaries (except innermost series) tipped by bristles usually 0.6–1.5 mm long; occurring elsewhere \_\_\_\_\_ **12. Xanthisma gracile**
13. Plants perennial, stems with woody bases; involucre glandular.
15. Bracts of peduncles imbricate and grading into phyllaries; stems nearly leafless above base \_\_\_\_\_ **13. Xanthisma junceum**
15. Bracts of peduncles few and not grading into phyllaries; stems leafy or leaves reduced near inflorescence.
16. Phyllaries strongly squarrose in upper half; leaves thickish, usually oblanceolate to spatulate with



- bluntly dentate to subentire margins; S Baja California Sur, Mexico \_\_\_\_\_ **11. Xanthisma arenarium**
16. Phyllaries with appressed to spreading apices; leaves thin, usually oblong to lanceolate with prominent teeth or lobes; SW Canada, W U.S.A.; N half of Mexico \_\_\_\_\_ **14. Xanthisma spinulosum**

**Xanthisma** DC. section **Xanthisma**

**Herbs** taprooted annuals, rarely biennials, 20–90 cm tall, taproot sometimes thickened. **Leaves** entire on upper stem, serrate below, pinnatifid to bipinnatifid near base, teeth or lobes usually with apiculate callosities, not bristle tipped. **Heads** radiate. **Involucre**s turbinate to hemispheric or campanulate. **Phyllaries** in 3–4 graduated series, the lower portion stalk-like, stiff, stramineous, enlarged above into an ovate to orbicular or depressed elliptic blade with a glabrous, green patch; apices acuminate or obtuse and cuspidate or broadly rounded, not bristle tipped. **Receptacles** alveolate, scales 0.2–2 mm long, mostly distinct. **Ray floret** corollas yellow. **Cypselae** distinctly dimorphic, 1.5–2.2 mm long, narrowly obovoid to oblong, walls thick with 8–16, often obscure ribs, sparsely pubescent; ray cypselae 3 sided; disc cypselae compressed laterally, generally 4 sided. **Pappus** similar in ray and disc florets, tawny; bristles 3–7 mm long, linear, dorsiventrally flattened basally, in 2 series.  $n = 4$ .

- 1. Xanthisma texanum** DC., Prodr. 5:95. 1836. TYPE: U.S.A. TEXAS. Bexar Co.: woods near Medina, May 1828. *J.L. Berlandier* 2039 (LECTOTYPE: IDC microfiche 800.787.I.7, G-DC! [designated by Semple 1974]; ISOLECTOTYPES: G-DC, GH, NY, US).

*Xanthisma texanum* DC. var. *berlandieri* A. Gray, Pl. Wright. 1:98. 1852. *Xanthisma berlandieri* (A. Gray) J.K. Small, Fl. S.E. U.S. 1184. 1903. TYPE: U.S.A. SOUTHERN TEXAS: *J.L. Berlandier s.n.*; on the Nueces, *A. Trécul s.n.* (SYNTYPES: GH).

KEY TO THE INFRASPECIFIC TAXA OF *XANTHISMA TEXANUM*

1. Blades of phyllaries somewhat expanded above the proximal stalk, mostly orbicular to depressed elliptic: dimensions above the widest part 1–2 mm long, 1.5–3.5 mm wide \_\_\_\_\_ **1a. X. texanum** subsp. **texanum**
2. Phyllary apices rounded with little or no flare 1 mm from the apex \_\_\_\_\_ **1b. X. texanum** subsp. **texanum** var. **texanum**
2. Phyllary apices obtusely cuspidate, flared distally, the ovate portion 1.5–2 mm long, 2–3 mm wide above the widest part \_\_\_\_\_ **1c. X. texanum** subsp. **texanum** var. **orientale**
1. Blades of phyllaries abruptly expanded above proximal stalk, mostly ovate: dimensions above the widest part 3.5–8 mm long, 2.5–5 mm wide \_\_\_\_\_ **1d. X. texanum** subsp. **drummondii**

**1a. Xanthisma texanum** DC. subsp. **texanum**

**1b. Xanthisma texanum** DC. subsp. **texanum** var. **texanum**

**1c. Xanthisma texanum** DC. subsp. **texanum** var. **orientale** Semple, *Rhodora* 76:14.



1974. TYPE: U.S.A. TEXAS. Hidalgo Co.: 13.5 mi N of Edinburg on U.S. hwy 183, 8 Jul 1970, W. Lewis 7642 (HOLOTYPE: MO).

**Id. *Xanthisma texanum* DC. subsp. *drummondii* (Torr. & A. Gray) Semple**, *Rhodora* 76:16. 1974. BASIONYM: *Centauridium drummondii* Torr. & A. Gray, *Fl. N. Amer.* 2:246. 1842. *Xanthisma texanum* DC. var. *drummondii* (Torr. & A. Gray) A. Gray, *Pl. Wright.* 1:98. 1852. *Xanthisma drummondii* (Torr. & A. Gray) Hooker f., *Curtis' Bot. Mag.* 33:t. 6275. 1877. TYPE: U.S.A. TEXAS: exact locality unknown, Nov 1835, T. Drummond 227 (LECTOTYPE: GH [designated by Semple 1974]; ISOLECTOTYPES: GH!, NY!).

*Xanthisma texanum* DC. subsp. *texanum* var. *orientale* Semple forma *rubrum* Semple, *Rhodora* 76:15. 1974. TYPE: U.S.A. TEXAS. San Patricio Co.: 0.5 mi E of Ingleside on Texas hwy 361, 13 Jun 1971, J.C. Semple 602 (HOLOTYPE: MO).

This polymorphic species has always been maintained distinct from other genera in the Tribe; in part due to the unique involucre. The relationship to members of *Machaeranthers* sensu lato was never seriously considered until data from DNA became available. According to Semple (1974) the following combination of features characterized the species: "heterocarpic fruit with a pappus of bristly scales only, fruit pubescence of long white ascending hairs, receptacle slightly convex with a persistent reticulate network of subulate scales." Interestingly, all of these characters are found in at least some of the taxa of this newly expanded genus.

Semple (1974) recognized two forms of variety *orientale*, the typical one having whitish lateral margins on the bracts and forma *rubrum* in which the lateral margins were red. Forma *rubrum* is said to be rare but is found mixed with the typical form throughout the range of var. *orientale*.

***Xanthisma* section *Blepharodon* (DC.) D.R. Morgan & R.L. Hartman, comb. nov.**  
BASIONYM: *Haplopappus* section *Blepharodon* DC., *Prodr.* 5:346. 1836, "*Aplopappus*," non *Blepharodon* Decne. in DC., 1844 [Asclepiadaceae].

*Machaeranthera* section *Blepharodon* (DC.) R.L. Hartman, *Phytologia* 68:443. 1990. TYPE: *Haplopappus gymnocephalus* DC., "*Aplopappus*" (lectotype designated by Hall 1928, from among the four species included).

*Eriocarpum* Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:320. 1840. *Haplopappus* section *Eriocarpaea* Benth. & J.D. Hook., *Gen. Pl.* 2:254. 1873, based on *Eriocarpum* Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:320. 1840. TYPE: *Eriocarpum grindelioides* Nutt.

*Machaeranthera* series *Originales* Cronquist & D.D. Keck, *Brittonia* 9:237. 1957, nom. illeg. (ICBN: 24.3).

**Herbs** taprooted annuals, biennials, or perennials, 3–50 cm tall, often with a much branched caudex or in loose colonies with stems arising from 3 to 10 or more elongate, branched rhizomes, 1.5–6 mm in diameter, from a woody rootstock. **Leaves** serrate or dentate, entire or rarely pinnatifid in a few species, teeth or lobes usually bristle tipped. **Heads** radiate or eradiate. **Involucres** depressed hemispheric to campanulate. **Phyllaries** in 3–6 graduated series, linear to lanceolate, the lower portion thickened, stramineous, the upper fourth to half her-



baceous or with a green or purple tinged strip or patch, stipitate glandular to canescent, appressed to reflexed; apices obtuse to long attenuate and usually bristly tipped. **Receptacles** alveolate, scales often present, 0.3–1.5 mm long, distinct or forming a reticulum. **Ray floret** corollas white, pink, purple, or lavender when present (yellow in *Xanthisma rhizomatum*). **Cypselae** distinctly dimorphic, (1–)1.5–3.5 mm long, narrowly obovoid to oblong, the walls thick with 6–18, often prominent ribs, often densely pubescent; ray cypselae obscurely 3 sided; disc cypselae compressed laterally. **Pappus** white to tawny; bristles 3.5–8 mm long, dorsiventrally flattened basally, in 2–4 graduated series, those of the ray florets often much reduced in length.  $n = 4, 8$ .

- 2. *Xanthisma blephariphyllum*** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus blephariphyllus* A. Gray, Pl. Wright. 1:97. 1852, "Aplopappus." *Eriocarpum blephariphyllum* (A. Gray) Greene, Erythea 3:14. 1895. *Machaeranthera blephariphyllo* (A. Gray) Shinnery, Field & Lab. 18:38. 1950. TYPE: U.S.A. Probably TEXAS: plains at the eastern base of the Guadalupe Mountains, 18 Oct 1849, C. Wright 288 (HOLOTYPE: GH!; ISOTYPE: NY!).

*Eriocarpum serratum* Greene, Bull. Torrey Bot. Club 25:119, pl. 331, fig. 3, 4. 1898. *Sideranthus serratus* (Greene) Standley, Contr. U.S. Natl. Herb. 13:222. 1910. TYPE: U.S.A. NEW MEXICO. Lincoln Co.: White Mountains, S fork of Tularosa Creek E of the Mescalero Agency, 6800 ft, 30 Jul 1897, E.O. Wootton 251 (HOLOTYPE: NDG!; ISOTYPES: B, K, MO!, NY!, RM!, UC!).

*Machaeranthera correllii* Shinnery, Field & Lab. 17:55. 1949. TYPE: U.S.A. TEXAS. Culberson Co.: Guadalupe Mountains, Pine Springs Canyon, 5700 ft, 15 Aug 1946, L. Shinnery 9059 (HOLOTYPE: SMU!).

- 3. *Xanthisma coloradoense*** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Aster coloradoensis* A. Gray, Proc. Amer. Acad. Arts 11:76. 1876. *Eriocarpum coloradoense* (A. Gray) Greene, Erythea 2:110. 1894, "coloradense." *Xylorrhiza coloradoensis* (A. Gray) Rydb., Bull. Torrey Bot. Club 32:124. 1905, "Xylorrhiza coloradensis." *Machaeranthera coloradoensis* (A. Gray) Osterhout, Torrey 27:64. 1927, "coloradensis," *Haplopappus coloradoensis* (A. Gray) R.L. Hartman ex R. D. Dorn, Vasc. Pl. Wyoming 295. 1988. TYPE: U.S.A. COLORADO: South Park near Hamilton, 4 Aug 1875, E.L. Greene 679 (LECTOTYPE, here designated from among syntypes: GH!).

*Xylorrhiza brandegei* Rydb., Bull. Torrey Bot. Club 32:124. 1905, "Xylorrhiza." *Machaeranthera coloradoensis* (A. Gray) Osterhout var. *brandegei* (Rydb.) T.J. Watson ex R.L. Hartman, Phytologia 68:444. 1990. TYPE: U.S.A. COLORADO: San Juan Pass, 1875, T.S. Brandege 1165 (HOLOTYPE: GH!; ISOTYPES: NY!, UC!).

- 4. *Xanthisma crutchfieldii*** (B.L. Turner) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera crutchfieldii* B.L. Turner, Phytologia 26:116. 1973. TYPE: MEXICO. NUEVO LEÓN: bare gypsum rock outcrop on south slopes, 17 mi E of San Roberto Junction, then 2 mi S, 24 Oct 1970, B.L. Turner & J. Crutchfield 6324 (HOLOTYPE: TEX!; ISOTYPE: MEXU!).

- 5. *Xanthisma grindelioides*** (Nutt.) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Eriocarpum grindelioides* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:321. 1840. *Haplopappus nuttallii* Torr. & A. Gray, Fl. N. Amer. 2:242. 1842, "Aplopappus,"



nom. nov., non *Haplopappus grindelioides* DC., Prodr. 5:348. 1836, "Aplopappus." *Aster nuttallii* (Torr. & A. Gray) O. Kuntze, Revis. Gen. Pl. 1:318. 1891, non Torr. & A. Gray, 1842. *Sideranthus grindelioides* (Nutt.) Britton in Rydb., Bull. Torrey Bot. Club 27:620. 1900. *Machaeranthera grindelioides* (Nutt.) Shinnery, Field & Lab. 18:40. 1950. TYPE: U.S.A. (WYOMING): on shelving rocks in the Rocky Mountain range, Oregon, s.d., *T. Nuttall* s.n. (HOLOTYPE: PH!; ISOTYPE: BM).

KEY TO THE VARIETIES OF *XANTHISMA GRINDELIOIDES*

1. Plants tufted, mostly 10–35 cm tall; leaves evenly distributed along the length of the stem, the margins often ciliate or spinulose-toothed but the bristles usually less than 1.5 mm long; peduncles less than 2 cm long, often leafy to the base of the capitulum; heads solitary or 2 to 5 per stem \_\_\_\_\_ **5a. *X. grindelioides* var. *grindeloides***
1. Plants densely caespitose, mostly less than 8 cm tall; leaves mostly crowded at the base of the plant, the margins lined with conspicuous, white bristles up to 4 mm long; peduncles 1–4 cm long, naked or with an occasional greatly-reduced leaf; heads mostly solitary \_\_\_\_\_ **5b. *X. grindelioides* var. *depressum***

**5a. *Xanthisma grindelioides* var. *grindeloides***

**5b. *Xanthisma grindelioides* var. *depressum*** (Maguire) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus nuttallii* Torr. & A. Gray var. *depressus* Maguire, Amer. Midl. Naturalist 37:144. 1947. *Machaeranthera grindeloides* (Nutt.) Shinnery var. *depressa* (Maguire) Cronquist & D.D. Keck, Brittonia 9:237. 1957. TYPE: U.S.A. UTAH. Millard Co.: Warm Point, in shallow gravelly and sandy soil, 5 mi SW of Desert Range Experiment Station Headquarters, 18 Jun 1941, *B. Maguire* 20859 (HOLOTYPE: NY!; ISOTYPES: GH!, UC!).

**6. *Xanthisma gymnocephalum*** (DC.) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus gymnocephalus* DC., Prodr. 5:346. 1836, "Aplopappus." *Aster gymnocephalus* (DC.) A. Gray, Proc. Amer. Acad. Arts 15:32. 1879, non (F. Ruprecht) B. Fedtschenko, 1915. *Eriocarpum gymnocephalum* (DC.) Greene, Erythea 2:109. 1894. *Machaeranthera gymnocephala* (DC.) Shinnery, Field & Lab. 18:40. 1950. TYPE: MEXICO: "Environs de Mexico," 20 Jul 1827, *J.L. Berlandier* 588 (LECTOTYPE, here designated: IDC microfiche 800. 867.III.6, G-DC!).

*Machaeranthera setigera* Nees, Linnaea 19:722. 1847. TYPE: "In terris Mexicanis," *De Berghes* s.n. (location of type unknown).

*Haplopappus phyllocephalus* DC. subsp. *primitivus* H.M. Hall, Publ. Carnegie Inst. Wash. 389:56, fig. 6. 1928. TYPE: MEXICO. MEXICO. Calcareous bluffs, Flor de Maria, 31 Jul 1890, *C.G. Pringle* 3179 (HOLOTYPE: UC!; ISOTYPES: GH!, NY!, PH!, SMU!, UC!).

**7. *Xanthisma gypsophilum*** (B.L. Turner) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera gypsophila* B.L. Turner, Phytologia 26:117. 1973. TYPE: MEXICO. COAHUILA: 14 mi S of Cuatro Ciénegas, then W 1.8 mi to actively blowing dunes of gypsum, 11 Apr 1970, *B.L. Turner* 6052 (HOLOTYPE: TEX!; ISOTYPES: MEXU!, MICH!).

**8. *Xanthisma johnstonii*** (S.F. Blake) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus johnstonii* S.F. Blake, Proc. Biol. Soc. Wash. 54:18. 1941, "Aplopappus." *Machaeranthera johnstonii* (S.F. Blake) B.L. Turner, Amer. J. Bot. 60:837. 1973. TYPE: MEXICO. COAHUILA: in dry heavy alkaline soil, 1 mi S of Hermanas, 22–24 Aug 1938, *I.M. Johnston* 7066 (HOLOTYPE: GH!; ISOTYPE: US!).



**9. *Xanthisma restiforme*** (B.L. Turner) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera restiformis* B.L. Turner, Amer. J. Bot. 60:836, figs. 1-5. 1973. TYPE: MEXICO. Coahuila: in gypsum soil 2.4 mi SW of Cuatro Ciénegas, 11 Apr 1970, B.L. Turner 6063 (HOLOTYPE: TEX!; ISOTYPES: MEXU!, MICH!).

**10. *Xanthisma rhizomatum*** (M.C. Johnston) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus rhizomatus* M.C. Johnston, Rhodora 63:177. 1961. *Machaeranthera heterophylla* R.L. Hartman, Phytologia 68:445. 1990, nom. nov., non *Machaeranthera rhizomata* A. Nelson & J.F. Macbride, Bot. Gaz. (Crawfordsville) 62:148. 1916. TYPE: MEXICO. NUEVO LEÓN: Saltillo-Matehuala highway, 5 mi N of junction of the side road to Galeana, 6000 ft, 8 Oct 1959, J. Graham & M.C. Johnston 4203 (HOLOTYPE: TEX!; ISOTYPES: KANU!, MEXU!).

***Xanthisma* section *Sideranthus*** (Nutt. ex Nees) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Sideranthus* Nutt. ex C. Nees in M. Wied-Neuwied, Reise Nord-America 2:440. 1841. *Dieteria* section *Sideranthus* (Nutt. ex Nees) Nutt. ex Walpers, Repert. Bot. Syst. 2:587. 1843. *Machaeranthera* section *Sideranthus* (Nutt. ex Nees) R.L. Hartman, Phytologia 68:456. 1990. TYPE: *Amellus spinulosus* Pursh.

*Machaeranthera* section *Stenoloba* R.L. Hartman, Phytologia 68:459. 1990. TYPE: *Eriocarpum stenlobum* Greene.

**Herbs** taprooted annuals, biennials, or perennials, 3-80 cm tall, sometimes with a much branched caudex. **Leaves** entire, serrate, dentate, or pinnatifid to deeply bipinnatifid, teeth or lobes usually bristle tipped, often markedly so. **Heads** radiate. **Involucres** broadly turbinate to depressed campanulate or hemispheric. **Phyllaries** in 4-8 graduated series, linear to narrowly oblong, the lower portion rigid, light green to stramineous, the upper fifth to half with a green patch or strip (sometimes blackish near apex), usually pubescent, often with glandular hairs, appressed to squarrose; apices obtuse to acuminate, usually tipped by a stiff and often pronounced bristle. **Receptacles** usually alveolate, scales 0.4-3 mm long, distinct or forming a reticulum. **Ray floret** corollas yellow. **Cypselae** often dimorphic, 1.5-3.2 mm long, elliptic to broadly obovate or obscurely and narrowly cordate, walls thin with 6-16 nerves or prominent ribs, glabrous to densely pubescent; ray cypselae usually rounded on dorsal edge, obscurely 3 sided, often asymmetrical, and slightly shorter; disc cypselae flattened laterally. **Pappus** white to tawny; bristles 3.5-6 mm long, slightly to moderately dorsoventrally flattened basally, in 2-4 markedly graduated series, those of the ray florets sometimes reduced in length.  $n = 2, 3, 4, 8$ .

**11. *Xanthisma arenarium*** (Benth.) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus arenarius* Benth., Bot. Voy. Sulphur 24. 1844, "Aplopappus." *Machaeranthera arenaria* (Benth.) Shinnars, Field & Lab. 18:40. 1950. TYPE: MEXICO. BAJA CALIFORNIA SUR: Cabo San Lucas, 1841, R. B. Hinds s.n. (HOLOTYPE: K, photo at DS!).

**12. *Xanthisma gracile*** (Nutt.) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Dieteria gracilis* Nutt., Proc. Acad. Nat. Sci. Philadelphia 4:22. 1848. *Haplopappus gracilis* (Nutt.) A. Gray, Pl. Fendler. 76. 1849, "Aplopappus," non T.S. Brandege, 1889.



*Aster dieteria* O. Kuntze, Revis. Gen. Pl. 1:315. 1891, based on *Dieteria gracilis* Nutt. *Eriocarpum gracile* (Nutt.) Greene, Erythea 2:109. 1894. *Sideranthus gracilis* (Nutt.) A. Nelson, Bot. Gaz. (Crawfordsville) 37:266. 1904. *Machaeranthera gracilis* (Nutt.) Shinnery, Field & Lab. 18:41. 1950. TYPE: U.S.A. NEW MEXICO: near Santa Fe, s.d., W. Gambel s.n. (HOLOTYPE: GH!; ISOTYPE: K).

*Haplopappus ravenii* R.C. Jackson, Amer. J. Bot. 49:123. 1962. TYPE: U.S.A. ARIZONA. Yavapai Co.: open oak grasslands near Johnson Wash, ca. 10 mi S of the Verde River, 8 Jun 1959, R.C. Jackson 2680 (HOLOTYPE: KANU!).

**13. *Xanthisma junceum*** (Greene) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus junceus* Greene, Bull. Calif. Acad. Sci. 1:190. 1885, "Aplopappus." *Eriocarpum junceum* (Greene) Greene, Erythea 2:108. 1894. *Sideranthus junceus* (Greene) A. Davidson & Moxley, Fl. S. Calif. 377. 1923. *Machaeranthera juncea* (Greene) Shinnery, Field & Lab. 18:40. 1950. TYPE: U.S.A. CALIFORNIA. San Diego Co.: Cleveland, s.d., M.K. Curran s.n. (lectotype designated from among two syntypes by Hall 1928 with no indication of location; it was not found in the following relevant herbaria: CAS, DS, NDG, UC, RSA).

**14. *Xanthisma spinulosum*** (Pursh) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Amellus spinulosus* Pursh, Fl. Amer. Sept. 2:564. 1813. *Haplopappus spinulosus* (Pursh) DC., Prodr. 5:347. 1836, "Aplopappus," non Phil., 1873, nec T.S. Brandege, 1889. *Starkea pinnata* Nutt., Gen. N. Am. 2:169. 1818, *nom. superfl.* *Machaeranthera pinnata* Shinnery, Field & Lab. 18:41. 1950, non *Machaeranthera spinulosa* Greene, 1899. *Dieteria spinulosa* (Pursh) Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:301. 1841. *Eriocarpum spinulosum* (Pursh) Greene, Erythea 2:108. 1894. *Sideranthus spinulosus* (Pursh) R. Sweet ex Rydb., Bull. Torrey Bot. Club 27:621. 1900. TYPE: U.S.A. [SOUTH DAKOTA. Lyman or Brule Co.: Reveal et al. 1999], in open prairies on the Missouri, 15 Sep 1804, M. Lewis s.n. (LECTOTYPE: PH! [designated by Hall 1928]; ISOLECTOTYPE: UC!).

*Diplopappus pinnatifidus* Hook. f., Fl. Bor.-Amer. 2:22. 1834. *Aster pinnatifidus* (Hook. f.) O. Kuntze, Revis. Gen. Pl. 1:313. 1891. *Machaeranthera pinnatifida* (Hook. f.) Shinnery, Sida 1:295. 1964, *nom. nov.*, non *Machaeranthera spinulosa* Greene, Pittonia 4:24. 1899. TYPE: CANADA. SASKATCHEWAN: Rocky Mountains near Jasper's Lake, s.d., Drummond s.n. (HOLOTYPE: K).

*Haplopappus spinulosus* (Pursh) DC. var. *canescens* A. Gray, P. Fendler. 75. 1849, "Aplopappus." TYPE: U.S.A. NEW MEXICO: between Santa Fe and the Rio del Norte, May 1847, A. Fendler 395 (HOLOTYPE: GH!).

*Eriocarpum wootonii* Greene, Bull. Torrey Bot. Club 25:120, pl. 330, fig. 1, 2. 1898. *Sideranthus wootonii* (Greene) Standley, Contr. U.S. Natl. Herb. 13:222. 1910. TYPE: U.S.A. NEW MEXICO: White Mountains, 19 Aug 1897, E.O. Wooton 518 (HOLOTYPE: NDG!; ISOTYPES: NY!, UC!).

*Sideranthus puberulus* Rydb., Bull. Torrey Bot. Club 27:622. 1900. TYPE: U.S.A. COLORADO. Chaffee Co.: Salida, s.d., C.B. Clarke 174 (HOLOTYPE: NY!; ISOTYPE: UC!).

*Sideranthus turbinellus* Rydb., Bull. Torrey Bot. Club 27:622. 1900. *Haplopappus spinulosus* (Pursh) DC. var. *turbinellus* (Rydb.) S.F. Blake, Contr. Gray Herb. 52:23. 1917, "Aplopappus." TYPE: U.S.A. IDAHO. Bannock Co.: Pocatello, 25 Aug 1892, A.I. Mulford s.n. (HOLOTYPE: NY!; ISOTYPE: UC!).

*Sideranthus machaeranthera* J.K. Small, Fl. S.E. U.S. 1186. 1903. TYPE: U.S.A. TEXAS: in dry soil, along the Brazos River, 1852, A.C. Schott 508a (HOLOTYPE: NY!; ISOTYPE: UC!).

*Sideranthus cotula* J.K. Small, Fl. S.E. U.S. 1186. 1903. *Haplopappus spinulosus* (Pursh) DC. subsp. *cotula* (J.K. Small) H.M. Hall, Publ. Carnegie Inst. Wash. 389:77. 1928. TYPE: U.S.A. OKLAHOMA (Indian Territory): Cherokee Town and vicinity, 1868, E. Palmer 442A (HOLOTYPE: NY!).



*Sideranthus laevis* Wooton & Standley, Contr. U.S. Natl. Herb. 16:180. 1913. *Haplopappus spinulosus* (Pursh) DC. subsp. *laevis* (Wooton & Standley) H.M. Hall, Publ. Carnegie Inst. Wash. 389:78. 1928. *Machaeranthera laevis* (Wooton & Standley) Shinnery, Field & Lab. 18:40. 1950. TYPE: U.S.A. NEW MEXICO. Eddy Co.: gypsum hills near Lakewood, 6 Aug 1909, E.O. Wooton s.n. (HOLOTYPE: US!; ISOTYPES: UC!, US!).

*Haplopappus texensis* R.C. Jackson, Rhodora 64:142. 1962. *Machaeranthera texensis* (R.C. Jackson) Shinnery, Sida 1:378. 1964. TYPE: U.S.A. TEXAS. Brooks Co.: sandy soil along railroad right-of-way about 7.5 mi S of Falfurrias, 7 Aug 1959, R.C. Jackson 2938-1 (HOLOTYPE: KANU!).

The following two binomials are not valid as the genus *Sideranthus* was a nomen nudum when the combinations were published: *Sideranthus pinnatifidus* Nutt., Fraser's Catalogue, no. 81, 1813, non *Aplopappus pinnatifidus* Nutt., 1840 and *Sideranthus spinulosus* (Pursh) Sweet, Hort. Brit., 227. 1826. Furthermore, *Eriocarpum australe* Greene (Erythea 2:108. 1894) although validly published has never been lectotypified. The relevant synonyms are: *Sideranthus australis* (Greene) Rydb., Bull. Torrey Bot. Club 27:621. 1900; *Haplopappus spinulosus* (Pursh) DC. subsp. *australis* (Greene) H.M. Hall, Publ. Carnegie Inst. Wash. 389:77. 1928; and *Machaeranthera australis* (Greene) Shinnery, Field & Lab. 18:42. 1950.

*Xanthisma spinulosum* "is an exceedingly complex, variable taxon. It is doubtful that any 'absolute' key can be constructed so as to recognize unequivocally the infraspecific categories proposed here. Instead, we have composed a key that attempts to recognize character *trends*, in combination, that serve to distinguish a given taxon from another, but the occasional (if not frequent) specimen will be found that keys to a given regional variety but belongs to yet another. However, if one accepts the exception and recognizes our account as an attempt to portray quite variable, *regional populations* and not as a key to individuals, then little trouble would be experienced in pinning a varietal name on this or that collection" (Turner & Hartman 1976). The following key is adapted from the aforementioned source.

#### KEY TO THE VARIETIES OF *XANTHISMA SPINULOSUM*

1. Involucres of pressed heads 15–25 mm wide, heads mostly solitary on elongate peduncles 2–15 cm or more long (shorter in Baja California, Mexico); herbs and subshrubs mostly (30–)50–100 cm tall; foliage relatively sparse, crowded below, internodes at mid-stem 0.5–2 mm or more long (short in Baja California, Mexico); W Colorado to S California and Arizona; Baja California, Mexico and vicinity.
2. Heads borne on elongate, leafy "peduncles," the upper leaves not much reduced, subspinose; subshrubs up to 100 cm tall \_\_\_\_\_ **14d. *X. spinulosum* var. *gooddingii***
2. Heads borne on relatively short, leafy "peduncles," the upper leaves not much reduced nor subspinose; perennial herbs, but often woody below or at the crown, mostly 30–60 cm tall.
3. Heads broadly campanulate; lower leaves generally 2–3 cm long, pinnatisect; W Colorado, adjacent Utah, New Mexico, and Arizona \_\_\_\_\_ **14f. *X. spinulosum* var. *paradoxum***



3. Heads broadly turbinate to campanulate; lower leaves 0.5–2 cm long, dentate to nearly incised leaves; Baja California, Mexico.
4. Involucres of pressed heads 22–25 mm wide; leaves large, decidedly incised; coastal islands \_\_\_\_\_ **14e. X. spinulosum** var. **incisifolium**
4. Involucres of pressed heads 15–20 mm wide; leaves small and nearly serrate or dentate; widespread on mainland \_\_\_\_\_ **14g. X. spinulosum** var. **scabrellum**
1. Involucre of pressed heads 8–15 mm wide, heads mostly 2 to 10 or more per stem on relatively terminal and lateral peduncles 0.5–2 cm long; herbs mostly 20–50 cm tall; foliage abundant and not much reduced upwards, internodes at mid-stem 0.2–0.5 cm or less long.
5. Stems stiffly erect, mostly unbranched, foliage glabrate or nearly so; heads nearly sessile; pappus bristles profuse, exceeding the disc corollas; South Dakota to N Texas \_\_\_\_\_ **14c. X. spinulosum** var. **glaberrimum**
5. Stems spreading to sprawling, usually much-branched, foliage variously pubescent, rarely glabrous; pappus less pronounced in the head, equaling the disc corolla; widespread, W Canada to SW U.S.A.; central Mexico.
6. Involucres of pressed heads 8–12 mm wide; stems equally leafy throughout; plants only rarely stiffly erect or woody at the base, mostly 10–40 cm tall; widespread \_\_\_\_\_ **14a. X. spinulosum** var. **spinulosum**
6. Involucres of pressed heads 12–16 mm wide; stems mostly leafy below, upper leaves much reduced giving the heads a “long-peduncled” appearance; plants stiffly erect and often woody at the base, mostly 30–50 cm tall; W Texas, S New Mexico, S Arizona; N Mexico \_\_\_\_\_ **14b. X. spinulosum** var. **chihuahuanum**

**(i) Xanthisma spinulosum** subsp. **spinulosum**

**14a. Xanthisma spinulosum** var. **spinulosum**

**14b. Xanthisma spinulosum** var. **chihuahuanum** (B.L. Turner & R.L. Hartman) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera pinnatifida* (Hook. f.) Shinnars var. *chihuahuana* B.L. Turner & R.L. Hartman, *Wrightia* 5:311. 1976. *Haplopappus spinulosus* (Pursh) DC. var. *chihuahuanus* (B.L. Turner & R.L. Hartman) K.N. Gandhi, *Phytologia* 69:276. 1990. TYPE: MEXICO. CHIHUAHUA: Sierra del las Monillas, ca. 16 mi SE of El Morreon on road to lake on Rio Conchos, 13 Jul 1972, A. M. Powell 2447 (HOLOTYPE: TEX!).

**14c. Xanthisma spinulosum** var. **glaberrimum** (Rydb.) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Sideranthus glaberrimus* Rydb., *Bull. Torrey Bot. Club* 27:621. 1900. *Sideranthus spinulosus* (Pursh) R. Sweet ex Rydb. var. *glaberrimus* (Rydb.) A. Nelson, in J.M. Coulter & A. Nelson, *Man. Bot. Rocky Mt.* 499. 1909. *Haplopappus spinulosus* (Pursh) DC. var. *glaberrimus* (Rydb.) S.F. Blake, *Contr. Gray Herb.* 52:24. 1917, “*Aplopappus*.” *Haplopappus spinulosus* (Pursh) DC. subsp. *glaberrimus* (Rydb.) H.M. Hall, *Publ. Carnegie Inst. Wash.* 389:77. 1928. *Machaeranthera pinnatifida* (Hook. f.) Shinnars forma *glaberrima* (Rydb.) McGregor, *Trans. Kansas Acad. Sci.* 60:162. 1957. *Machaeranthera pinnatifida* (Hook. f.) Shinnars var. *glaberrima* (Rydb.) B.L. Turner & R.L. Hartman, *Wrightia* 5:311. 1976. TYPE: U.S.A. NEBRASKA. Thomas Co.: Middle Loup River near Thedford, 19 Aug 1893, P.A. Rydberg 1403a (HOLOTYPE: NY!; ISOTYPES: GH!, US!).

**(ii) Xanthisma spinulosum** subsp. **gooddingii**

**14d. Xanthisma spinulosum** var. **gooddingii** (A. Nelson) D.R. Morgan & R.L.



Hartman comb. nov. BASIONYM: *Sideranthus gooddingii* A. Nelson, Bot. Gaz. (Crawfordsville) 37:266. 1904. *Haplopappus gooddingii* (A. Nelson) Munz & I.M. Johnston, Bull. Torrey Bot. Club 49:44. 1922, "Aplopappus." *Haplopappus spinulosus* Pursh) DC. subsp. *gooddingii* (A. Nelson) S.F. Blake, Contr. U.S. Natl. Herb. 25:543. 1925, "Aplopappus." *Machaeranthera pinnatifida* (Hook. f.) Shinnery subsp. *gooddingii* (A. Nelson) B.L. Turner & R.L. Hartman, Wrightia 5:313. 1976. *Machaeranthera pinnatifida* (Hook. f.) Shinnery var. *gooddingii* (A. Nelson) B.L. Turner & R.L. Hartman, Wrightia 5:314. 1976. TYPE: U.S.A. NEVADA: "The Pockets," 30 Apr 1902, L.N. Goodding 667 (HOLOTYPE: RM!, ISOTYPE: US!).

*Sideranthus viridis* J.N. Rose & Standley, Contr. U.S. Natl. Herb. 16:19, pl. 15. 1912. TYPE: MEXICO. SONORA: Pinacate Mountains, 21 Nov 1907, D.T. MacDougal s.n. (HOLOTYPE: US!, ISOTYPE: UC!).

**14e. *Xanthisma spinulosum* var. *incisifolium*** (I.M. Johnston) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus arenarius* Benth. var. *incisifolius* I.M. Johnston, Proc. Calif. Acad. Sci., ser. 4, 12:1190. 1924, "Aplopappus." *Haplopappus spinulosus* (Pursh) DC. subsp. *incisifolius* (I.M. Johnston) H.M. Hall, Publ. Carnegie Inst. Wash. 389:75. 1928. *Machaeranthera pinnatifida* (Hook. f.) Shinnery var. *incisifolia* (I.M. Johnston) B.L. Turner & R.L. Hartman, Wrightia 5:315. 1976. *Machaeranthera incisifolia* (I.M. Johnston) G.L. Nesom, Phytologia 69:112. 1990. TYPE: MEXICO. BAJA CALIFORNIA: S San Lorenzo Island, 9 May 1921, I.M. Johnston 3529 (HOLOTYPE: CAS!, ISOTYPES: NY!, UC!).

**14f. *Xanthisma spinulosum* var. *paradoxum*** (B.L. Turner & R.L. Hartman) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera pinnatifida* (Hook. f.) Shinnery var. *paradoxa* B.L. Turner & R.L. Hartman, Wrightia 5:314. 1976. *Haplopappus spinulosus* (Pursh) DC. var. *paradoxus* (B.L. Turner & R.L. Hartman) Cronquist, Intermountain Fl. 5:199. 1994. TYPE: U.S.A. COLORADO. Montrose Co.: Paradox, 21 Jun 1912, E. P. Walker 147 (HOLOTYPE: NY!, ISOTYPES: DS!, GH!, RM!, US!).

**14g. *Xanthisma spinulosum* var. *scabrellum*** (Greene) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Eriocarpum scabrellum* Greene, Erythea 2:108. 1894. *Haplopappus spinulosus* (Pursh) DC. var. *scabrellus* (Greene) S.F. Blake, Contr. Gray Herb. 52:24. 1917, "Aplopappus." *Haplopappus spinulosus* (Pursh) DC. subsp. *scabrellus* (Greene) H.M. Hall, Publ. Carnegie Inst. Wash. 389:74. 1928. *Machaeranthera scabrella* (Greene) Shinnery, Field & Lab. 18:42. 1950. *Machaeranthera pinnatifida* var. *scabrella* (Greene) B.L. Turner & R.L. Hartman, Wrightia 5:314. 1976. TYPE: MEXICO. BAJA CALIFORNIA: foothills Los Angeles Bay, Dec 1887, E. Palmer 539 (HOLOTYPE: NDG!, ISOTYPE: NY!).

*Haplopappus arenarius* Benth. var. *rossii* I.M. Johnston, Proc. Calif. Acad. Sci., ser. 4, 12:1191. 1924, "Aplopappus." TYPE: MEXICO. BAJA CALIFORNIA SUR: on margin of a gypsum mesa, San Marcos Island, 12 May 1921, I.M. Johnston 3627 (HOLOTYPE: CAS!, ISOTYPE: US!).

**15. *Xanthisma stenolobum*** (Greene) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Eriocarpum stenolobum* Greene, Erythea 2:109. 1894. *Haplopappus stenolobus* (Greene) H.M. Hall, Publ. Carnegie Inst. Wash. 389:65. 1928. *Machaeranthera stenoloba* (Greene) Shinnery, Field & Lab. 18:40. 1950. TYPE: MEXICO. CHIHUAHUA: Sierra Madre, Arroyo Ancho, 16 Oct 1887, C.G. Pringle 1303 (HOLOTYPE: NDG!, ISOTYPES: GH!, NY!, PH!).

**16. *Xanthisma wigginsii*** (S.F. Blake) D.R. Morgan & R.L. Hartman, comb. nov.



BASIONYM: *Haplopappus wigginsii* S.F. Blake, Proc. Biol. Soc. Wash. 48:169. 1935, "Aplopappus." *Machaeranthera wigginsii* (S.F. Blake) R.L. Hartman, Phytologia 68:458. 1990. TYPE: MEXICO. BAJA CALIFORNIA: Sierra San Pedro Mártir, 18 Sep 1930, I. L. Wiggins & D. Demaree 4914 (HOLOTYPE: US!).

**Xanthisma** section **Havardii** (R.C. Jackson) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Haplopappus* section *Havardii* R.C. Jackson, Univ. Kansas Sci. Bull. 46:479. 1966. *Machaeranthera* section *Havardii* (R.C. Jackson) R.L. Hartman, Phytologia 68:458. 1990.

**Herbs** taprooted annuals, 15–45 cm tall. **Leaves** serrate or dentate, often coarsely so, teeth blunt or terminating in stiff callosities, not bristle-tipped. **Heads** radiate. **Involucres** broadly turbinate. **Phyllaries** in 5–7 graduated series, linear to narrowly oblong, the lower portion rigid, stramineous, the upper fifth to half with a green patch or strip, densely glandular, appressed; apices obtuse to acute. **Receptacles** alveolate, scales 0.1–0.5 mm long, mostly distinct. **Ray floret** corollas yellow. **Cypselae** essentially similar, 2.5–3 mm long, oblong or narrowly elliptic, sometimes slightly asymmetrical, flattened laterally, walls thin with 12–14 barely discernible nerves, sparsely pubescent. **Pappus** similar in ray and disc florets, white; bristles 5–7 mm long, filiform, not dorsiventrally flattened basally, in 2–3 poorly defined series.  $n = 4$ .

**17. Xanthisma viscidum** (Wooton & Standley) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Sideranthus viscidus* Wooton & Standley, Contr. U.S. Natl. Herb. 16:180. 1913. *Haplopappus viscidus* (Wooton & Standley) S.F. Blake, J. Wash. Acad. Sci. 28:486. 1938. *Machaeranthera viscida* (Wooton & Standley) R.L. Hartman, Phytologia 68:459. 1990. TYPE: U.S.A. NEW MEXICO. Eddy Co.: near Hope, 3 Aug 1905, E.O. Wooton s.n. (HOLOTYPE: US!).

*Haplopappus havardii* Waterfall, Rhodora 45:352. 1943. *Machaeranthera havardii* (Waterfall) Shinnars, Field & Lab. 18:40. 1950. TYPE: U.S.A. TEXAS. Culberson Co.: 9 mi E of Van Horn, s.d., U.T. Waterfall 4153 (HOLOTYPE: GH!; ISOTYPES: ARIZ!, MO!, NY!).

**Arida** D.R. Morgan & R.L. Hartman, comb. et stat. nov. BASIONYM: *Machaeranthera* section *Arida* R.L. Hartman, Phytologia 68:446. 1990. TYPE: *Machaeranthera arida* B.L. Turner & D.B. Horne.

**Herbs** taprooted annuals or rarely short lived perennials (often much branched, rhizomatous, forming vegetative rosettes in *A. blepharophylla*), 10–60(–80) cm tall. **Stems** erect to ascending or sprawling, often much branched, glabrous to variously pubescent with glandular and nonglandular hairs. **Leaves** alternate; entire, dentate, lacerate to deeply pinnatifid or bipinnatifid, glabrous to densely pubescent with glandular or nonglandular hairs, apices, including lobes and teeth, apiculate to bristle tipped, bristles 0.1–1 mm long. **Heads** radiate or eradiate. **Involucres** turbinate to depressed hemispheric. **Phyllaries** in 4–8 imbricate series, graduated in length, appressed, spreading, or reflexed, glabrous or moderately to densely pubescent with glandular or nonglandular hairs; bases indurate to herbaceous, apices herbaceous, margins sometimes scarious.



**Receptacles** indistinctly alveolate, convex, naked or nearly so, or (in *A. blepharophylla*) with scales up to 0.5 mm long. **Ray florets** pistillate, fertile (absent in *A. carnosa*); corollas light to dark blue. **Disc florets** bisexual, fertile, corollas yellow,  $\pm$  funnellform, tubes and limbs generally glabrous, lobes 0.3–0.5 mm long, glabrous to minutely pubescent. **Cypselae** of ray and disc florets somewhat dimorphic, narrowly oblong, moderately to densely pubescent; thin walled, with 5–11 filiform nerves per face, 1–3.2(–4) mm long, those of ray florets, if present, obscurely 3 sided, rounded abaxially, of disc florets only slightly compressed laterally; pappus white or whitish (tawny in *A. blepharophylla*), of ray florets 1/3 to nearly equaling length of disc florets; bristles minutely barbellate, in 2–3 poorly differentiated series, at most somewhat dorsi-ventrally flattened and dissimilar in width near base, bases not to slightly overlapping, mostly 2.5–4.5(–5) mm long.  $n = 5$ .

Four of the nine species that are here included in *Arida* (*A. blepharophylla*, *A. parviflora*, *A. riparia*, and *A. turneri*) were included in molecular investigations of *Machaeranthera* s.l. (Morgan & Simpson 1992; Morgan 1997, 2003). The conflicting relationships supported by cpDNA and nrDNA for these species suggested substantial reticulate evolution among the four species and with species of *Dieteria*, *Pyrrocoma*, and *Xanthisma*, complicating efforts to produce a taxonomy that best reflects current understanding of the systematics of *Arida*.

In classifying the species of *Arida*, one issue to consider is the proper taxonomy for *A. blepharophylla*. Chloroplast DNA and nrDNA supported conflicting relationships for this species (Fig. 1), suggesting that it has experienced reticulate evolution (Morgan 1997, 2003). Since the taxonomy of *A. blepharophylla* should match its evolutionary history as closely as possible, it would be desirable to base its classification on what kind of reticulate evolution has occurred. As described by Morgan (1997), there are two major possibilities. First, because *A. blepharophylla* exhibits characteristics of both parental lineages, it could have originated through hybrid speciation; the best treatment in this situation might be to establish *A. blepharophylla* as a monospecific genus descended from, but separate from, both parental lineages.

The second evolutionary possibility is that *A. blepharophylla* is a close relative of *A. riparia* that has acquired chloroplast DNA from the ancestor of *Xanthisma gymnocephalum*; the best treatment in this case might be to classify it with *A. riparia*. Here we choose the latter disposition. According to nrDNA evidence, the nuclear relationships of *A. blepharophylla* are with *A. riparia*. In addition, the majority of its characteristics, including chromosome number and fruit morphology, are shared with *A. riparia* rather than with *X. gymnocephalum* (Nesom et al. 1990). It is possible that *Arida blepharophylla* is a hybrid species, but in our view additional genetic data would be necessary to convincingly demonstrate the occurrence of hybrid speciation. In the absence of such data we propose that *A. blepharophylla* be considered a close relative of



*A. riparia* that has experienced chloroplast introgression, and that its taxonomy reflect this history.

With *Arida blepharophylla* classified with *A. riparia*, the next question is whether the nine species of *Arida* should all be maintained in the same genus. If *A. blepharophylla* is placed with *A. riparia* as described above, cpDNA evidence would support keeping all the species together because it supported a group composed of *A. parviflora*, *A. turneri*, and *A. riparia* (Fig. 1). However, nrDNA evidence separated these four species into two lineages (Fig. 1). As described in detail by Morgan (2003), there are two primary explanations for this conflict, both involving reticulate evolution. The first explanation considers the alliances supported by nrDNA to be closer to the true species relationships. The corresponding classification would split *Arida* into two parts.

The second explanation considers the alliances supported by cpDNA to be closer to the species relationships for *Arida*. In supporting the group composed of *A. parviflora*, *A. turneri*, and *A. riparia*, cpDNA evidence suggested that the two lineages of *Arida* are closest relatives. In this case, the corresponding taxonomy would keep the two lineages together, retaining all species of *Arida* in the same genus. This is the classification adopted here because, in addition to cpDNA, several additional pieces of evidence support this treatment. All species of *Arida* have  $n = 5$ , all that have been investigated produce flavones, and hybridization experiments suggest much genetic similarity between the two lineages (Turner & Horne 1964; Turner et al. 1975; Stucky 1978; Hartman 1976, 1990; Nesom et al. 1990). This array of characteristics unites the species of *Arida* and distinguishes them from other taxa in the *Machaeranthera* complex; we interpret the conflicting results from nrDNA data as resulting from nrDNA introgression, as explained by Morgan (2003).

The following key is based in part on data in Hartman (1976, 1990), Nesom (2003), Nesom et al. (1990), and Turner (1986). It includes the new species *Arida matturneri* (Turner & Nesom 2003).

#### KEY TO THE SPECIES OF ARIDA

1. Ray cypselae pappose (heads eradiate in *A. carnos*).
2. Leaves entire to toothed.
  3. Ray florets absent \_\_\_\_\_ **3. *Arida carnos***
  3. Ray florets present.
    4. Plants annual; leaf margins entire and glabrous or with 1–8 teeth per side, each spinulose tipped; involucre hemispheric, 10–16 mm wide when fresh; phyllaries linear lanceolate to oblong lanceolate, narrowly acute to acuminate or attenuate \_\_\_\_\_ **8. *Arida riparia***
    4. Plants perennial, rhizomatous, forming vegetative rosettes; leaf margins essentially entire with 8–20 cilia or bristles per side, cilia 0.4–0.8(–1.5) mm long; involucre turbinate, 5–8 mm wide when fresh; phyllaries oblong ovate to obovate, broadly acute to short acuminate \_\_\_\_\_ **2. *Arida blepharophylla***



2. Leaves (at least some) pinnatifid to bipinnatifid.  
 5. Receptacles 8–11 mm wide; phyllary apices spreading to reflexed \_\_\_\_\_ **9. *Arida turneri***  
 5. Receptacles 2–7 mm wide; phyllary apices mostly appressed \_\_\_\_\_ **7. *Arida parviflora***
1. Ray cypselae epappose (except in occasional plants).  
 6. Mid-stems essentially glabrous or with few sessile glands.  
 7. Leaves deeply pinnatifid; SW Colorado, N New Mexico, Utah, and E Arizona; Chihuahua and Coahuila, Mexico \_\_\_\_\_ **7. *Arida parviflora***  
 7. Leaves above basal rosette, if present, entire or toothed.  
 8. Stems 10–45 cm long, weakly ascending to procumbent; SW Sonora, Mexico \_\_\_\_\_ **4. *Arida coulteri***  
 8. Stems 50–80 cm long, erect; W Texas \_\_\_\_\_ **6. *Arida matturneri***
6. Mid-stems densely glandular pubescent.  
 9. Involucres 3–6 mm tall, 5–10 mm wide; mid-stems densely glandular, also with longer, crisp, nonglandular hairs interspersed; S Nevada, S California, S Arizona; N Sonora, Mexico \_\_\_\_\_ **1. *Arida arizonica***  
 9. Involucres 6–8 mm tall, 10–15 mm wide; mid-stems densely glandular, nonglandular hairs absent; N Baja California Sur and adjacent W Sonora, Mexico \_\_\_\_\_ **5. *Arida crispa***

**1. *Arida arizonica*** (R.C. Jackson & R.R. Johnson) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera arizonica* R.C. Jackson & R.R. Johnson, *Rhodora* 69: 476, fig. 1. 1967. TYPE: U.S.A. ARIZONA. Pima Co.: Oregan Pipe Cactus National Monument, low, rocky hillsides and sandy soils around Quitobaquito Springs, 31 Mar 1962, R.C. Jackson & R.R. Johnson 3043-1 (HOLOTYPE: KANU!; ISOTYPES: ARIZ!, KANU!).

*Machaeranthera arida* B.L. Turner & D.B. Horne, *Brittonia* 16:324. 1964. *Machaeranthera coulteri* (A. Gray) B.L. Turner var. *arida* (B.L. Turner & D.B. Horne) B.L. Turner, *Phytologia* 61:144. 1986. TYPE: U.S.A. CALIFORNIA. San Bernardino Co.: Mesquite Valley, 1.7 mi SW of Kingston, 2600 ft, 15 May 1941, C.B. Wolf 10635 (HOLOTYPE: DS!; ISOTYPES: NY!, TEX!, UC!).

*Machaeranthera ammophila* Reveal, *Bull. Torrey Bot. Club* 97:172. 1970. TYPE: U.S.A. NEVADA. Nye Co.: Amargosa Desert, on the W edge of Ash Meadows, 0.3 mi W of Carson Slough, 21 Aug 1968, J.L. Reveal & N.H. Holmgren 1882 (HOLOTYPE: US!; ISOTYPES: GH!, NY!, RM!).

**2. *Arida blepharophylla*** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Aster blepharophyllus* A. Gray, *Pl. Wright*. 2:77. 1853. *Machaeranthera gypsitherma* G.L. Nesom, Vorobik, and R.L. Hartman, *Syst. Bot.* 15:638. 1990, nom. nov., non *Machaeranthera blephariphylla* (A. Gray) Shinnars, *Field & Lab.* 18:38. 1950. TYPE: U.S.A. NEW MEXICO. Hidalgo Co.: in subsaline soil, Las Playas Springs, 7 Oct 1851, C. Wright 1164 (LECTOTYPE: GH! [designated by Nesom et al.1990]; ISOLECTOTYPES: CGE, GH!, MO!, NY!, P, PH!).

**3. *Arida carnosa*** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Linosyris carnosa* A. Gray, *Pl. Wright*. 2:80. 1853. *Aster carnosus* (A. Gray) A. Gray ex W. B. Hemsley, *Biol. Cent.-Amer., Bot.* 2:120. 1881, non J.-B. Gilibert, 1781. *Leucosyris carnosa* (A. Gray) E.L. Greene, *Fl. Francisc.* 384. 1897. *Machaeranthera carnosa* (A. Gray) G.L. Nesom, *Phytologia* 67:439. 1989. TYPE: MEXICO. SONORA: W of Chiricahui Mountains, Sep 1851, C. Wright 1187 (HOLOTYPE: GH!; ISOTYPES: PH!, US!).

*Bigelowia intricatus* A. Gray, *Proc. Amer. Acad. Arts* 17:208. 1882. *Aster intricatus* (A. Gray) S.F. Blake, *J. Wash. Acad. Sci.* 27:378. 1937. *Machaeranthera carnosa* (A. Gray) G.L. Nesom var.



*intricata* (A. Gray) G.L. Nesom, *Phytologia* 82:106. 1997. TYPE: U.S.A. CALIFORNIA: Mohave Desert, at Lancaster Station, s.d., *C.C. Parry* s.n. (HOLOTYPE: GH!).

**4. *Arida coulteri*** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Psilactis coulteri* A. Gray, *Pl. Fendler* 72. 1849. *Machaeranthera coulteri* (A. Gray) B.L. Turner & D.B. Horne, *Brittonia* 16:322. 1964. TYPE: MEXICO. SONORA: probably the vicinity of Guaymas, n.d., *T. Coulter* 295 (HOLOTYPE: GH!).

**5. *Arida crispa*** (T.S. Brandegeee) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Psilactis crispa* T.S. Brandegeee, *Proc. Calif. Acad. Sci.*, ser. 2, 2:169. 1889. *Machaeranthera crispa* (T.S. Brandegeee) B.L. Turner & D.B. Horne, *Brittonia* 16:321. 1964. TYPE: MEXICO. BAJA CALIFORNIA SUR: alkaline soil, San Joaquine, San Ignacio, 1 Apr 1889, *T.S. Brandegeee* s.n. (HOLOTYPE: UC!; ISOTYPES: GH!, US!).

**6. *Arida mattturneri*** B.L. Turner & G.L. Nesom, *Sida* 20:1418. 2003. TYPE: U.S.A. TEXAS. Presidio Co.: ca. 2.2 mi NNW of Ruidosa in "Blumberg Canyon," (ca. 30° 00' 45" N, 104° 44' 00" W), 20 Jul 2003, *M.W. Turner* 100 (HOLOTYPE: TEX; ISOTYPES: NY!, SRSC).

**7. *Arida parviflora*** (A. Gray) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera parviflora* A. Gray, *Pl. Wright* 1:90. 1852. *Aster parviflorus* (A. Gray) A. Gray in W.H. Brewer & S. Watson, *Bot. California* 1:322. 1876, non C. Nees, 1818, nec W. Darlington, 1826. *Aster parvulus* S.F. Blake in Tidestrom, *Contr. U.S. Natl. Herb.* 25:563. 1925. TYPE: U.S.A. TEXAS: "collected in expedition from W Texas to El Paso, N. Mex.," May–Oct 1849, *C. Wright* 271 (HOLOTYPE: GH!; ISOTYPES: NY!, US!).

*Machaeranthera tanacetifolia* (Kunth) C. Nees var. *pygmaea* A. Gray, *Pl. Wright* 2:74. 1853. *Aster tanacetifolia* Kunth var. *pygmaeus* (A. Gray) A. Gray, *Syn. Fl. N. Amer.* 1(2):206. 1884. *Machaeranthera pygmaea* (A. Gray) Wooton & P.C. Standley, *Contr. U.S. Natl. Herb.* 16:189. 1913. TYPE: U.S.A. NEW MEXICO: near El Paso, 1851, *C. Wright* 1395 (HOLOTYPE: GH!; ISOTYPES: NY!, US!).

**8. *Arida riparia*** (Kunth) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Aster riparius* Kunth, *Nov. Gen. Sp.*, folio ed., 4:72. 1818. *Machaeranthera riparia* (Kunth) A.G. Jones, *Syst. Bot.* 8:85. 1983. TYPE: MEXICO: "In humidis juxta lacum Cuiseo. . . alt. 900 hex." n.d., *F.W.H.A. von Humboldt & A.J.A. Bonpland* 4308 (HOLOTYPE: P; ISOTYPES: B-W, P).

*Aster sonorae* A. Gray, *Pl. Wright* 2:76. 1853. *Machaeranthera sonorae* (A. Gray) Stucky, *Amer. J. Bot.* 65:132. 1978. TYPE: U.S.A. SOUTHERN ARIZONA: low valley W of the Chiricahui Mountains, Sep 1851, *C. Wright* 1163 (HOLOTYPE: GH!; ISOTYPES: CGE, PH!, US!).

**9. *Arida turneri*** (M.L. Arnold & R.C. Jackson) D.R. Morgan & R.L. Hartman, comb. nov. BASIONYM: *Machaeranthera turneri* M.L. Arnold & R.C. Jackson, *Syst. Bot.* 3:209. 1979. TYPE: MEXICO. CHIHUAHUA: 3.3 mi N of Meoqui, along highway 45, 1 Aug 1964, *R.C. Jackson* 4005 (HOLOTYPE: TTC!).

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